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MARTIN MARKGREN

FUGITIVE REACTIONS IN

AVIAN BEHAVIOUR

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CONTENTS

ESCAPE BEHAVIOUR

Fugitive behaviour in avoiding disturbing phenomena
with a quality of individuality and mostly
with pronounced direction
in time and space

Definition of Fugitive Action

Those actions are fugitive by which an animal orientates itself in such a relation of time and space to a phenomenon with an objective and/ or subjective quality of adversity that there is an increased probability of avoiding or decreasing the dangerous, harmful or unfavourable effect of that phenomenon on the animal.

Fugitive actions may take place *in vacuo*.

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INTRODUCTION

Modern ethology is a young science with its roots in both animal psychology and experimental zoophysiology (BIERENS DE HAAN 1937, 1947, PIERON 1941). The pioneer work was done by LORENZ and TINBERGEN. The latter has gathered the ethological problems into a coherent whole and has treated in one volume the most important European and American literature dealing with ethological subjects (TINBERGEN 1951). The aim of ethology is to observe, describe, analyse and interpret animal behaviour. In analysing behaviour, the actions of the animals have been postulated as reactions to internal and external stimuli. With that assumption, behaviour has been provoked experimentally by external incitements. The purpose of analysis is, however, not only to deduce the causal relations and the biological significance but also to elucidate the organisation and the functional morphology of the actions. TINBERGEN, emphasizing the complexity of behaviour, has also shown the value of field study in making a sensitive interpretation of the single actions in the continuous flow of behaviour. LORENZ, in his foreword to "The Herring Gull's World" by TINBERGEN (1953), writes:

It is a fact that organic life in general, and animal behaviour in particular, is "directed"; but it is also a fact that it obeys the laws of natural causation, just as much as inorganic nature. It can, accordingly, only be understood if both these facts are equally kept in mind. One of the few people who really do this is NIKO TINBERGEN. It is also characteristic that he cannot be classified either as field observer or as laboratory man: he is both at once.

But primarily he is a hunter. He likes to stalk and watch and sit in hides. Unlike myself, he does not want to keep and breed animals, but prefers to study them in their wild haunts, the wilder the better.

In their observation and analysis of bird behaviour both TINBERGEN and LORENZ have taken the greatest interest in the central behaviour complex of the reproduction activity. In European and American ornithology migration research has shown a tendency in the last few years to evolve as a science on the limits between field ethology and ecology. Thus, for instance, RUDEBECK (1950A), in dealing with the central problems of migration, has repeatedly returned to an analysis of migratory behaviour and its actual causes. As a matter of fact, this is typical of Fennoscandian migration literature (cf. also SVÄRDSON 1949 C). Probably in the future migration observers will have something to learn from the ethologists, and vice versa. If ethologists have hitherto taken but little interest in migratory behaviour, the same cannot be said about the interest in escape reactions of birds. The famous experiments with bird models used by LORENZ and TINBERGEN (1948) are fundamental for our knowledge of escape reactions. As

regards the hunting behaviour of predatory birds and the behaviour of the hunted birds, RUDEBECK (1950 B, 1951) has made an outstanding analysis of the matter and has given a thorough discussion of the literature. This is perfect field ethology!

In the present paper on birds' escape reactions, the author makes an attempt at an introductory discussion of the problems of *fugitive reactions*. For the sake of simplicity the well-defined escape reaction of taking wing will be discussed especially. The paper is based on field observations of wild birds and simple experiments on birds in the field.

SUBJECT, PROBLEMS, METHODS, LOCALITIES

1. Choice of Subject and Definition of Problems

The birds' world is composed of dangerous and non-dangerous things. The latter, constituting a world rich in nuances from useful to completely unvalued things, are responded to with varying behaviour. The dangerous phenomena, on the other hand, are met with *fighting* or *escape behaviour*. Some behaviours include both reaction elements as, for instance, the mobbing behaviour (cf. LACK 1953, TINBERGEN, 1953, ALTMANN 1956). All these single behaviours are thought to consist of innate, simple reflex movements, complicated instinctive acts, orientation movements and innate reactions more or less modified by learning processes (LORENZ 1927, 1931, 1953, TINBERGEN 1951, 1953). The whole scale of varying "fright" and escape reactions, from neurophysiological and hormonal phenomena, intention movements and alarm notes to bodily escape or the reverse, the immobility reaction or crouching, constitutes a functional unit. However, the author in the following discussion of fugitive behaviour has chosen to abstract the taking-wing reaction and to treat it as an isolated phenomenon; this has been done for several reasons.

1. The comparative aspects demand isolation of well-defined behaviour elements, a description which fits the taking-wing reaction well.

2. The very moment of taking wing is easily observable and in no way ambiguous. It is always possible to find out, without any doubt, if the birds just take flight or behave in some other way. Further, in that behaviour it is easy to classify the reacting birds in chronological order, which is of great value in distinguishing between primary reactions and secondary, i.e. induced, behaviour.

3. Taking-wing behaviour as a reaction on the appearance of predatory birds plays a great part in the Scanian localities where the author has worked. This is due both to the considerable concentrations of species and specimens of birds, even birds of prey, during the yearly migration, and to the surveyability of the localities.

4. Finally, the choice of subject is motivated by the interest arising from early impressions. Thus, the boy's uncomplicated wonder over common gulls and lesser blackbacked gulls in their noisy taking wing over the last great lanes in the ice in late spring has developed into the desire to ask concrete questions.

The matter to be considered may be expressed in the following questions:

(1 a) To *which disturbances* do the respective bird species react? (This formulation is similar to the next.)

(1 b) *Which species* react to the respective disturbances?

(2)   *How* do the respective species react to the respective disturbances? (Questions (1 a) and (1 b) include individual variations.)

(3)   How are the reactions arranged and organized as animal *locomotive activity* and as the performance of (geometric) *morphological patterns* and as objective *responses to physical influences?*

(4)   What are the *biological significance* and the *origin* of the reactions?

(5)   What psychical experiences do these birds have?

(6)   What are the releasing signals?

2. Choice of Methods of Study

In order to obtain some answers to the above questions close field observations of the wild birds must be carried out. Some adapted experiments may be made in the study of isolated reactions. The author has made both experiments and field studies of wild birds. TINBERGEN (1951, 1953) has pointed out the necessity of studying both the isolated elements and the entirety of the behaviour, and the value of observations of animals in their natural environments. In this connection the present author wishes to mention the importance of noting the migratory activity or the tendencies of such activity. Thus, for instance, when migrating birds are resting and exhibit escape reactions on some disturbance, their escape behaviour is often succeeded by migration or migratory activity, especially if the weather situation is in some way favourable to migration. Obviously the diurnal foraging movements of the herring gulls, in SW. Sweden usually a sort of shift to inland foraging localities, are often initiated by an escape reaction. On such occasions their behaviour may consist of three different kinds of activity, namely: (1) *escaping*, (2) *migratory* activity, as, for instance, soaring as a reaction to upwind thermal currents, (3) the *foraging* shift. To the observer there is a continuous flow of behaviour. The question is, then, whether there is a succession in time or a simultaneity in the reactions of the birds. If there is a coincidence of reactions, an important question is whether or not there is also a mutual interdependence of reactions. These questions will be discussed later in this paper. They have been mentioned in this chapter in order to emphasize the necessity of study of behaviour in the field.

Field study needs no explanation. It means close watching, observing and noting the behaviour observed. As to the experiments concerning our subject, the following possibilities may be mentioned:

A. Experiments on wild birds in the field.

B. Experiments on domestic birds.

C. Experiments on wild birds in captivity.

Types A and B have been used in this study. Regarding the experimental tools in use, another subdivision of the experiments has to be made and the following devices used:

(1) *Living or stuffed animals.*

(2) Simple *models* of animals with stress on varying elements of morphology or colour.

(3) *Acoustic phenomena.*

(4) The observer himself produces the disturbances in some way or other, for instance, by imitating some elements of a certain animal behaviour.

(5) *Artificial* disturbances of different kinds. Valuable results may be obtained by any combination.

The combination of experiments on B or C with (1) has given important and even celebrated results (cf. TINBERGEN 1951). The combination of C with (1) and (2) has also been used with success (cf. KRAMER & VON ST. PAUL 1951). HARTLEY (1950) and ALTMANN (1956) have made interesting studies with the combination of A with (1) and (2). The present author has worked only with type A in combination with the varieties (3), (4) and (5). These combinations are used partly with the intention in some respects to complete the results reached by other combinations. The performance of the study will be discussed later in this paper. In view of the methods chosen, it will be necessary to consider the choice of localities.

3. The Choice of Localities for the Field Study

The choice was easy because an important locality is situated in the vicinity of Malmö and Lund, i.e. the locality of Sjölunda. The study was performed in the following areas or at the following places; the places are mentioned in the order of their significance for the present paper.

(1) Sjölunda and the meadows of Arlöv. This is a locality on the flat seashore N. of Malmö in Scania, S. Sweden (Oct. to May since 1943).

(2) Some other localities on the W. shore of Scania.

(3) Localities at the Scanian Lakes.

(4) Other Scanian localities.

(5) Localities in N. Fennoscandia.

(6) Localities in Denmark, Germany, Holland and France.

There are certain advantages in working in localities where migrating birds rest during their non-reproductive periods. In the first place, it means a fine view of large concentrations of birds, and secondly, there are possibilities of eliminating behaviour determined by the reproductive activities.

4. The Scope of the Observations

In all respects the field work was performed most completely and thoroughly in the Sjölunda area. The study there was done early in the morning and sometimes also in the evening and at other times of the day, when necessary. As a rule the observations comprised:

(1) Counting or computation of the resting birds.
(2) Migration observation in the traditional sense.
(3) Behaviour study, especially as regards reactions to meteorological elements and reactions to the "disturbances".

5. Sources of Error in the Study and the Reliability of the Observations

The reliability of the observations is very dependent on what the observer knows about potential errors and how to avoid them. That knowledge is likely to increase in the course of the study.

When the actual observation material was transferred to paper, the author became conscious of the fact that the earliest material is not of the same value as the observations made in later years. In Sjölunda continuous notations of observed escape reactions have been made immediately at the time of the observations since 1949. At other localities immediate notations on the subject were not the rule until the spring of 1953. In many cases (before 1953), for that reason, notations made by degrees, after the observations, were so scanty that they have been omitted here. The observation technique has also undergone some evolution during the study. The same must be said of the direction of the study. Thus some of the older material has been excluded, because it is at present not of current interest. This is not to say that those earlier observations are of no value.

Some of the sources of error are due to variations in the behaviour, either of individuals or of groups.

A. *Differences owing to Individual Variations*

1. Variations in physiological condition of the birds. The reactions of birds suffering from disease, very cold weather, lack of food or rest or the reactions of hunted birds may not without criticism be compared with the reactions of normal and intact birds.

2. Variations owing to periodical activation of groups of instincts. The escape behaviour of birds may show special features during the *reproduction* period and during *migratory* activity.

3. Individual behaviour differences without known causes. For instance, in a flock of birds (crows or gulls) some of the birds may present mobbing behaviour often, others seldom and still others perhaps never. Thus, observed absence of mobbing behaviour may be representative of the observed bird or birds but not of the species or not even of the population as a whole.

4. Variation in the behaviour of one and the same bird from time to time. The variation of reaction may be caused by a summation effect or, on the contrary, by a fatiguing effect of the reaction mechanism.

B. *Differences owing to Variations in the Behaviour of Bird Populations or Groups*

1. One bird population "knows by experience" a bird (of prey) that is harmless to the population, whereas another population is lacking that experience. If,

then, the second population shows escape reaction to the harmless bird, the first population none, obviously the reactions of both populations must be known in order to enable a discussion of what is innate or not. Good examples are the differences in reactions to *Ardea cinerea* or *Pandion*, where these species are breeding and where they are not.

2. In one population a predatory bird is known from experience only by its hunting, whereas to another bird population it is known also by activities without actual dangers. The reactions of the second population or group will be more complicated than those of the first group. The gulls, ducks and crows of Sjölunda for instance, will present escape reactions to flying eagles and peregrine falcons in more than 99 % of cases, whereas the fugitive behaviour of the same species at the lakes of S. Scania, where eagles (*Aquila* and *Haliaeetus*) are common wintering birds, will be more dependent on the actual behaviour of the predator (cf. TINBERGEN 1953). Thus it is necessary to study the behaviour of different populations of birds.

Two more behaviour differences of another character cause errors of quite another order.

C. *Variations of Behaviour owing to the Individual Evolution of the Bird*

The adult bird may present escape reaction in a different way than the young bird or it may react with mobbing or fight.

D. *Seeming Variations*

This expression covers a wide field of possible errors. In observing birds in motion, it is very easy to get a wrong idea of distances, heights, directions and angles of the motions, especially if the sight is poor or if the observer is not quite familiar with the locality. It is also easy to overlook an expected behaviour, if it is presented only as an intention movement. For that reason, noted negative behaviour, i.e. absence of expected behaviour, may in some instances be of little value to the discussion.

Some types and examples of possible errors are mentioned above, most of which are avoided after experience. On the other hand, new difficulties will appear to the observer with new problems to be solved. When it comes to interpreting the observed behaviour, problems and sources of errors of quite another order will arise. Obviously the objective reality that may appear the same to the sense organs of both birds and the human observer is interpreted in a different way by bird and man. That statement may perhaps seem trivial, but it is a fact that is easily overlooked, as anthropomorphism is our first self-evident and spontaneous working hypothesis in our efforts to understand the animals. Gradually the anthropomorphism may appear in still more refined shape but it will never be entirely eliminated.

EXTERNAL PHENOMENA CAUSING FUGITIVE (AND/OR HOSTILE) BEHAVIOUR IN BIRDS

1. "The Disturbance" and the Concept of Disturbance

In this paper the concept of disturbance is used in the meaning of external phenomena causing primary (non-induced) escape reactions in the birds. "A disturbance" is thus first an objective reality characterized by a general accessibility. In the object of the disturbance there appears a contemporaneous objective phenomenon without general accessibility, viz. a neurophysiologic process of perceiving the disturbance. The perception by the object of the disturbance, the object that is the simultaneous perceiving subject, will provide the material of a potential subjective reality, namely, a probable visual–auditory–sensitive imagination or apprehension of the optic-acoustic phenomenon. Using an anthropomorphism, we can say that the birds' apprehension of an external phenomenon is its "conception" and "interpretation" of the objective phenomena. The word "interpretation" is not used here in the sense of thought only as an indication of a selective apprehension (cf. TINBERGEN 1951). The subjective imagination possibly exists as an independent phenomenon. These potential independent imaginations are of interest for the interpretation of vacuum activities (cf. TINBERGEN 1951, POULSEN 1953).

2. The Systematic of the Disturbances

The disturbances are either natural or artificial phenomena.

A. *Natural Disturbances*

These disturbances are usually of an optic-acoustic character. The disturbed bird will get a visual auditory perception of, for instance, a predatory bird, a man or a mammal.

(a) *Predatory birds as disturbances*

In discussing avian predators systematically as regards their behaviour, it would be desirable to treat them by species, as is done by RUDEBECK (1950B, 1951). This allows a sensitive consideration of the richness of behaviour variations in predatory birds, both as regards species and as regards individuals. The hunting behaviour of a number of Fennoscandian species of birds of prey is discussed by the present author in a paper in Swedish (MARKGREN 1959). A discussion by species, however, would be too comprehensive for the present paper, as

already the Scanian predatory avifauna consist of at least 20 species. Not seldom the birds of prey in discussion are divided into *fast-moving* and *slow-moving* predators (DAANJE 1941, HARTLEY 1950), a division that is of a certain significance for our subject. To this classification there will, however, be added a schematic basis for division as regards mode of motion.

SLOW MOTION

1. *Soaring.* This behaviour is observed by the author in 30 European predatory species and in 5 species of *Strigiformes.*

2. *Gliding.* A rectilinear flying movement mostly seen in the larger birds of prey in upwinds and in moderate horizontal winds.

3. *Hovering.* In upwinds this may be practised by any predator.

FAST MOTION (ATTACK FLIGHT)

1. *Surprise attack.* Such behaviour is typical of *Accipiter nisus* and *Circus* but is also found in *Accipiter gentilis, Aquila, Falco,* and in *owls.*

2. *Rectilinear acceleration.* In *Falco rusticolus, F. peregrinus, F. subbuteo* and *F. columbarius* this behaviour is common, but it may also be seen in both *Aquila* and *Haliaeetus* and not seldom in *Accipiter gentilis.*

3. *Upward curved acceleration.* In *Falco peregrinus,* sometimes in *F. rusticolus, F. subbuteo, F. Columbarius* and in *Accipiter gentilis* this behaviour appears. There is a forward motion with a strong upward component in a flight with lashing, accelerated wing beats and with a slightly upward-tilted body plane. The prey, a single bird or a flock, is thus forced upward. That effect will be increased as the pursuer alternates with attempts to seize the prey by doing a loop or a roll with extended legs and claws (cf. RUDEBECK 1950 B, 1951). If the prey is not captured, it will try to escape by a downward deflection. Then the predator often changes to the following behaviour:

4. *Swooping.* The swooping attack is a typical but not predominant mode of hunting in *Falco peregrinus, F. rusticolus, F. subbuteo, F. columbarius,* and *Accipiter gentilis.* It is more seldom used by other species, but has been observed by the author in *Aquila chrysaëtos, A. clanga* and *(mirabile dictu)* in *Haliaeetus* (cf. RUDE-BECK 1950 B, 1951). The behaviour in question was also observed by the author in *Hieraaetus,* where it is probably typical.

As is shown by RUDEBECK (1950 B, 1951), some very special modes of hunting must be considered of interest to the ethological discussion, not least as regards the reactions of the prey. Here especially should be mentioned the peculiar attack flight seen in *Falco columbarius* (and less pronounced in *F. subbuteo*), i.e.

5. *"Thrush flight"* (or "Swallow-flight") (RUDEBECK 1951, MARKGREN 1959). RUDEBECK (1951) also mentioned a behaviour, in the merlin, that can be designated:

6. *"Mobbing attack"* (or "pseudo-mobbing"). This behaviour has been observed by the present author not only in the merlin but in some few instances also in the

other birds of prey as a reaction to non-predators, thus in *Accipiter gentilis* as reaction to *Corvus corax*. The "quarry" may be injured (MARKGREN 1959).

Here must be mentioned another behaviour observed by the author in predatory birds of Swedish Lapland:

7. *Hunting close above the ground.* The typical behaviour is seen in *Falco rusticolus* and consists of fast lashing flight alternating with short gliding moments. It is also observed as behaviour in the following species (*mutatis mutandis*) *F. peregrinus* and *F. columbarius* (cf. RUDEBECK 1951) and in *Aquila chrysaëtos*. This behaviour is found in all the *Circus* species, as pointed out (*in litt.*) by K. CURRY-LINDAHL, who observed it often in the Belgian Congo. This mode of hunting is often seen to be successful. Unfortunately, however, the author has not had the opportunity of examining prey captured, as it has been taken from the ground and not eaten on the spot. This way of hunting may be an adaptation to prey hiding on the ground, either mammals or birds or both. (This behaviour and its significance may call for study.)

Finally another behaviour of predators must be mentioned that is not characterized as either slow or fast motion but rather as a pronounced mode of activity.

STEADY MIGRATION FLIGHT

This is seen in any bird of prey species at Falsterbo in September and October from about 9 a.m. to about noon on days with maximum migration of raptorial birds. It is typically a rectilinear flight with some gliding and steady making of height over the sea. It is obviously a reaction to the embryonic thermal currents in connection with moderate winds from about SW. (from the sea and opposite to the direction of migration) over Falsterbo. To predatory birds with a strong migratory motivation, this situation seems to be an effective releaser of migration flight at Falsterbo. It must be mentioned here that these migrating predators obviously do not act as disturbances on those occasions at Falsterbo.

(b) *Man as disturbance.*

Man as a disturbance requires a brief presentation and discussion.

The human beings that have acted as causes of fugitive behaviour in birds at Sjölunda should be divided into three categories: category I the author, category II the scavengers working on a rubbish tip in the Sjölunda area (where herring gulls and crows are common), and category III occasional visitors.

Category I. (1) The author has moved in the area parallel to the concentrations of resting birds, either at a distance greater than the critical distance for observable fugitive intention movements of the birds (provoking arm movements are avoided) or at a distance just touching the critical value, in order to induce a differentiated behaviour as to species and individuals. (2) The author has moved in directions forming an angle with the bird concentration (which is usually parallel to the shore line). This movement was usually carried out with the intention to disturb. (3) The movements were performed at a distance safely outside the critical zone.

The following motions were practised by the author: short runs parallel to the bird concentration and towards it, jumps without arm movements, vertical arm movements along the body, throwing movements as when throwing a javelin or a discus, pushes or blows, walking *on all fours*, creeping and worming movements (the two last-mentioned movements were often used inside the critical zone in order to come close to the birds). (4) The critical zone was exceeded by walking in a curved line concavely, cutting the long axis of the bird concentration, i.e. partly flanking the birds circuitously. (5) The movement was fully circuitous, its actual curve form modified by the localisation of the bird flock(s). (6) The author advanced in zigzags. (7) Repeated curved movements with the convex side directed towards the birds. (8) As in (7) but rectilinear with the obtuse angle towards the birds. (9) As in (8) but at an acute angle (the disturbing effect is more pronounced in (9) than in (7) and (8)). (10) The author tried to hide by moving about among the scavengers. Then the disturbance was certainly most intense at the initial moment, but it was never fully eliminated, even when continued for some hours.

Category II. The movements of the scavengers are usually slow and measured. Runs do not occur. On the other hand, work is carried out with tools such as spades, spits, shovels, brooms and rakes. Throwing movements do occur sometimes. A great deal of the work is done mechanically. In severe cold the author has, however, sometimes seen the scavengers practising jumps and forced arm wheelings (buffetings). To these buffetings the herring gulls have reacted by taking wing, which is of interest, as this category otherwise rarely acts as a disturbance.

Category III. Hunters or shooters, strollers, people loading sand or seaweed and boys playing belong to this category. Here the behaviour is quite variable as regards direction of walk, mode of movement, acoustic effects and so on. This category is important as disturbance but of little use for scientific purposes because of its heterogeneity.

Some few bird species show surprisingly little escape reaction to man, irrespective of his behaviour (*Perisoreus infaustus, Pinicola, Loxia leucoptera, Phalaropus lobatus*). Most other birds present intense reactions even at a considerable distance. Man is thus an important disturbing phenomenon to birds, but as shown above far from unequivocal. It is this complexity that is rather the characteristic feature of man. Whereas the pine grosbeak, which reacts sensitively to *Accipiter, Surnia, Glaucidium* or cats and dogs, will "ignore" a man throwing his gloves and running at it to provoke it into taking wing, most other birds will react immediately to a man who runs or makes throwing movements. This is of interest on account of what is known of animal behaviour as reactions, usually not to situations or complicated phenomena as a whole but to single elements. Now, whereas the run or walk towards the birds is typical of most predatory animals, throwing is seldom found below the sub-order *Anthropoidea* and is characteristic of man. The throwing behaviour as in throwing either a javelin or a discus and the related blow or push behaviour is characterized by a certain speed and acceleration of the motion.

To crows, ducks, gulls and many other birds the typical throw or blow is a disturbance, whereas exactly the same motions without the speed and the acceleration are not (with two exceptions, (1) when the man is standing motionless and is thus not observed by the birds, who may have come close to him, and (2) when the man is so near to the birds, that any movement will mean a new position and a distance of another order). Even on slinging food to the birds, a typical throw will be a disturbance. These statements will be of interest in our discussion of some experiments. Man as a non-specific disturbance will be treated below.

(c) *Non-avian animals as disturbances*

Especially the "dangerous animals", i.e. the predators, will act as typical disturbances. Fugitive behaviour in *Aves* has been observed by the author as reactions to *Canis lupus* (by a brood of ptarmigan to a running wolf) to *Vulpes, Alopex, Lutra, Mustela erminea* and *M. nivalis*, to *Lepus, Rattus norvegicus, Sciurus* (and to dogs and cats). As a rule, the intensity of the escape reaction has been in some proportion to the magnitude of the disturbing animal or to its intensity of behaviour. A sudden appearance also will be a matter of disturbance, regardless of species.

(d) *Man and non-avian animals as non-disturbances*

In considering our subject we have to remember that a bird may show escape reaction to a member of its own species and, on the other hand, may ignore a predator, for instance, if it has proved to be harmless. Learning, adaption and selection processes must be taken into account. The attitude of most birds to the herbivorous animals is non-fugitive, if these do not present strange behaviour or are not directly menacing, e.g. just about to tread on the bird, and so on. How much is then innate and what is learned? That question is not so very simple to answer. A brood of *Lagopus* may, for instance, react by taking wing for a walking fox, a reindeer or a man at just the same short distance. But it may run for the reindeer and sit close for man and fox at another distance. The reactions of birds to harmless animals are variable. The fugitive behaviour presented at a short distance is probably entirely innate reactions, whereas the absence of escape reaction to harmless animals is likely to be mostly dependent on an absence of releasing stimuli and not on learning processes.

The avian escape reaction to a man throwing is an observable fact. Its nature, however, is not clear. Probably it is partly, perhaps entirely innate, although not of necessity primarily an escape reaction to man. (This problem will be discussed below.)

The absence of fugitive reaction to man, however, is often a secondary, non-innate behaviour. The behaviour may vary somewhat from an indifferent attitude (like the herring gulls at Sjölunda towards the scavengers) to an interested intimacy (Lorenz 1943, 1953). Usually the training of birds to inhibit fugitive behaviour to man is carried out by providing food for them, and it is amusing to

see adult birds begging or even showing sexual display to the man providing food (cf. LORENZ 1953).

As regards natural but non-specific human disturbances see below.

(e) *Natural non-biologic disturbances*

From our point of view there is a systematic difference between living and non-living disturbances. To the animals there is also a difference between these two groups of phenomena, a difference that would be essential to an extremely anthropomorphic creature, i.e. an animal which could imagine the concept of life. But the animals known to modern ethology do not have this capacity of thought. Disregarding, however, what the animal is possibly thinking on reacting, the elements of behaviour are the same, following identical patterns, whereas the entirety of the behaviour is likely to have a more complicated form in reactions to biological disturbances, i.e. to animals themselves able to modify their behaviour.

Although it would be wholly correct from both the logical and the linguistic point of view to speak of animals escaping non-living dangers, such as heavy precipitations, forest fire, a cold wind, the tide and so on, yet the escaping concept is so associated with behaviour as reactions to predatory animals, that it will perhaps facilitate the discussion to use the wider conception *fugitive behaviour* in that connection and to reserve the escaping concept for just the single elements of reactions. Elements of fugitive behaviour as reactions to weather phenomena will be mentioned as they play a great part in avian migration. Among these weather phenomena the following elements are the most important in that connection: temperature, wind, humidity, snow precipitation (and a snow cover). Fall of temperature, especially in connection with high humidity and strong winds, has a certain effect here. Thus a physiological temperature factor is hidden in the relative humidity and the air movement. During early spring migration a shallow ground inversion of temperature may act as a releaser of reversed migration. The birds singing on migration flight may be found to grow silent and suddenly rise away from the cold air over the sometimes snow-covered fields and return out over the sea.

Non-biologic disturbances other than weather elements are, for example, some marine phenomena such as rising water (for instance, at high tide, cf. TINBERGEN 1953).

B. *Artificial Disturbances*

The avian attitude to motor (or steam) vehicles is not wholly unequivocal. In some members of *Anseriformes* and *Charadriiformes*, for instance, there may be no escape reaction to moving cars or trains if not going quite close to the birds, whereas some waders, such as *Vanellus*, most gulls and some species of *Passeriformes* such as *Corvus corax* and *Sturnus vulgaris*, seem to react with escape to the appearance of cars and trains, although they may *learn* to inhibit the fugitive

behaviour. Of course, any bird species may by training inhibit escape from harmless vehicles, just as bad experiences may accentuate an innate fugitive reaction. Thus, for instance, in the few years when waders have been seen to make an attempt to winter in Scania (such as 1951-52, 1958-59; cf. MARKGREN in manuscript), the escape reactions of lapwings to trains have in time been reduced to almost nothing. An engine with suddenly escaping steam is, however, an effective disturbance, probably mainly of an acoustic nature. The report of a shot is another acoustic phenomenon, the disturbing effect of which is well known (cf. EDELSTAM & RAMEL 1956). The phenomena mentioned above are just some few examples from the multitude of artificial disturbances. To the bird, however, there is nothing non-natural, only a richness of phenomena, some of which stimulate to foraging, resting, mating, fighting, escaping behaviour or only to flying or soaring behaviour. There may be many simultaneous impulses or just one single or even sometimes no external impulse. That question belongs, however, to experimental neurophysiology.

From the systematic point of view the *model experiments* should be treated just here. Nevertheless in order to facilitate the discussion it is necessary first to consider the concept of critical zones or distances in avian fugitive behaviour.

C. *The Critical Zones for Hostile and Fugitive Behaviour*[1]

When a *Larus argentatus* at the remote edge of a flock takes wing and escapes from a *Falco peregrinus* or a *Haliaeetus*, we say that the approaching predatory bird has reached the *gull's critical distance for decided escape reaction* to the actual disturbance. Yet, before that happens, some other critical zones may have been passed by the predator, thus stimulating other less outstanding reactions in the gull.

Providing that the bird of prey is approaching quite visibly, there will be a certain distance at which it will stimulate the gull to the first observable reactions, such as the slight movements of eye, neck and head for observation, then the *anxiety posture*, the fugitive *intention movements*, the *alarm call* and finally *the rising* and *the flying in escape*. In fact, any subject (of a certain minimum size), moving up close to a bird, will be met with hostile or fugitive behaviour, i.e. fighting, mobbing, display or escape, if that subject is not the offspring, an accepted sexual partner, or a member of a social group, such as a foraging, sleeping, fugitive or migratory group. In social birds or rather in the social behaviour of birds, the critical distance for intraspecific hostile and fugitive reactions may be reduced by inhibitory impulses to a minimum value about zero, especially in the non-reproductive periods. Thus the author has observed groups of birds in close bodily contact in the following situations: (1) birds *resting* in cold and hard winds, usually migrating birds of the species *Fringilla montifringilla*, *Calidris alpina*, *Tringa totanus*, *Vanellus vanellus*, *Chlidonias nigra*, *Sterna paradisaea*, *Larus minutus*, *L. ridibundus* and *L. canus*, (2) birds *foraging* in winter, not seldom mixed flocks of *Fringilla*, *Emberiza*, *Alauda* and sometimes *Anthus pratensis*, (3) birds *in sleep* (cf. MOUNTFORT 1957). In migration flight, as well as in foraging migratory flight, the critical distance (the intra-

[1] *Cf.* HEDIGER *1934*.

specific distance) of *social* birds is usually minute. It is thus interesting to compare the group pattern of *corvidae* on migration or foraging flight. *Corvus corax* will migrate in family groups, and *C. corone cornix* as single birds simultaneously but not in flocks, whereas *C. frugilegus* will appear in tight flocks, as also *C. monedula*. The jackdaws, when mated, will migrate in flocks with the single pairs discernible. The concept of "critical distance" just discussed is by no means identical with the concept of "territory". A critical distance in the above sense, as regards the bird itself, may rather play a part in the delimitation of a territory. TINBERGEN in his work on the herring gull (1953) has stated that the biological function of an avian territory may be (1) to space out the males ensuring maximum efficiency of germ cells, (2) to provide a nesting hole. Finally, he suggests that the use of the territory is (3) to ensure a food supply for the young and as regards the herring gull, (4) for defence. Point (3) is not generally accepted. As regards that problem, the author has in the course of a few years made simple experiments with passerine birds during their breeding. The results of these experiments, which are to be treated later on, point to the existence of an avian territory for food-supply, just in the sense that TINBERGEN has suggested.

As will be understood from the discussion above, the value of a critical distance is no constant quantity. It will rather show individual variation and variations in time. Probably, however, it is quite invariable under equal circumstances in one and the same group or population of birds. The value of the critical zone is obtainable by observation. Thus, the critical zone for observable reactions of a bird flock to man is limited and defined outwards by the fact of any bird of the flock showing signs of observing the man, whereas the interior limitation is defined by the first observable change to a reaction of a greater intensity, i.e. anxiety or escape reactions. In this paper the exterior limit is the one which is of interest.

D. *Arranging Disturbances Experimentally*

The performance of the experiment is in many ways dependent on the tools used. *Live animals* in captivity may, for instance, be used as tools, where the wild animals do not supply enough material for a study. Here that situation is not of current interest. *Animal-dummies or models* are much used for the study of escape reactions.

The famous experiments by GOETHE, KRÄTZIG, LORENZ and TINBERGEN with models of flying gliding birds do not need any presentation. (For discussion see TINBERGEN 1951.) KRAMER & VON ST. PAUL (1951) made laboratory experiments on *Pyrrhula pyrrhula* with gypsum models, hairy or feathered clumps and stuffed birds. In these experiments the bullfinches showed anxiety responses to objects having (1) a hairy or feathered texture, (2) a convex shape, (3) a coloured surface. Bad experiences play a part. HARTLEY (1950) presented an interesting series of experiments made in the open air on wild birds with different models of owls. He found that many species of passerine birds recognized dummy owls by the same combination of visual characters, namely, if they were (1) owl-like in outline,

(2) solid in contour, (3) coloured in browns and/or greys, or in tone contrasts of these colours, (4) patterned in a system of spots, streaks or bars. The conclusions were based on observed mobbing behaviour. ALTMANN (1956) has also made field experiments with stuffed owls. He outlines a method for determining whether mobbing behaviour is learned or innate and proposes that mobbing is innate in at least one American warbler species.

Now, returning to the classical model experiments by LORENZ and TIN-BERGEN, we find that escape reactions are released by a gliding bird model with a short neck. The experiments were made by moving the model but without "wing movements" of the bird models. We may perhaps add the feature of soaring or sailing. As it would be complicated to arrange models which move their wings, we might compare the results with field experiments. How do birds react to characters of necks, wings, wing movements and motion curves of other birds?

The neck

1. *Short neck*. A short neck is typical of *Alcidae*. They fly, however, with wing movements and motion curves quite different from those of *Falconidae*. The author has not observed escape reactions in birds to flying members of *Alcidae*.

2. *Long neck*. In *Ardeidae* and *Ciconiidae* the long neck is an outstanding feature. These birds fly in a somewhat eagle-like manner. In ducks and gulls the author has seen escape reaction to flying *Ciconia ciconia*, *Botaurus stellaris*, and *Ardea cinerea* with its neck still extended. Probably the wing movements, the rhythm and the outlines of the wings thus play a part as releasers of escape reactions.

The wings

See above under *The neck*.

Movements, the motion curve and the speed

Some observations of escape reactions in small passerine birds and waders to flying *Phasianus colchicus* and *Columba palumbus* in display mating flight may be interpreted as examples of reactions to motion curves perhaps in combination with a wing feature, the sailing and the speed of the movement.

The author has made some experiments with simple tools. Stones and small sticks were thrown into the air. (The author was hidden in a shed.) To the falling sticks, crows and herring gulls sometimes showed escape reactions. It was the author's intention to make a bow and arrows of different shapes for shooting, thus developing the experiment. This was, however, never done. Another experiment proved to be very useful. In the author's notes it has been called "örn-provet", i.e. "the eagle test". In this paper this experiment will be called the "arm test".

The "arm test" experiment

When the author as a boy, together with other boys, none of whom possessed a field glass, was creeping about bird watching, it was noted by chance that ducks

and many other birds were sensitive to arm movements and not necessarily to swift motions, but rather to slow movements with extended arms, such as pointing movements, and not necessarily in the direction of the bird. In fact, these slow movements were by chance the precursors of the "arm test". When new bird species or a new population has to be tested, the following actions are carried out:

(1) Testing the birds for the critical distance.

(2) Moving to a distance greater than the critical.

(3) After a *pause* testing the birds with the movements described in chapter II, (b), category I, (3).

(4) Pause and check. As a rule 5 min. and never less than 30 sec.

(5) On the same spot, performing the "arm test" in a strict sense. Two variations, (a) waving the arms in a slow rhythm at about the wing rhythm of a *Haliaeetus* and standing upright, (b) as in (a) but standing bent forward.

(6) After 4–5 wavings checking what and how many birds have reacted. Then going on with the wavings till all birds have reacted primarily or secondarily (or as with *Cygnus*, until it is obvious that there will be no positive reaction).

When the "arm test" was made on a well-known population, such as the herring gulls at Sjölunda during the winter, the author later abbreviated the experiment by starting with (5).

More than 1500 tests were made and noted by the author. At Sjölunda at least one test per day was made during those months when daily observations had to be done. As regards variations (a) and (b) of the test, there has not been any observable difference in the results.

The reactions of the birds to the "arm test" are discussed in the next chapter.

THE FUGITIVE (AND HOSTILE) RESPONSES OF BIRDS TO EXTERNAL DISTURBING PHENOMENA

1. On Possible Reactions and their Distribution in the Species

From a zoological point of view the question can never be asked, *whether or not* an animal will react to environment, since its existence as a member of Regnum Animale makes it a link in the endless chain of mutual reactions of living species. Whether the animal be an amoeba or a mammal the question has to be put as to modality, quantity and quality of reaction. The organisation level of the amoeba enables the discerning of eatable, non-eatable and unpropitious things and the ingestion, elimination and escaping reactions.

What are the possible reactions on the avian organisation level to a potential danger to the species? We find that the bird has to remain *in loco*, take shelter or resist the danger in some way.

A. *Escape in Situ—Escape to the Ground or into the Water*

(a) *Remaining on the ground*

Many birds pass through an early stage of individual evolution, where the typical reaction to a disturbance is to sit close to the ground, behaviour which may seem to be a primitive or infantile (neothenic) reaction. In brooding birds disturbed on their nests, the sitting reaction may result in a sleeping behaviour. In hunted waders (*Calidris alpina* and *Tringa*) the author has in some instances observed a change from escape flight (as a reaction to *Falco* and *Accipiter nisus*) to alighting and sleep reaction. The waders, having been hunted, were probably getting tired. Nevertheless, their behaviour probably was a sort of displacement action. These examples perhaps indicate a relation in some instances between the fugitive sitting reaction and displacement sleep reactions. (For discussion of sleep behaviour see TINBERGEN 1951.)

In brooding birds disturbed on the nest, two conflicting drives are likely to occur, the drive to sit on the eggs and the instinct of escape. Then the displacement sleep is one way out of the tension. Other display behaviours of birds will be discussed by the author in a paper on behaviour in some arctic and boreal birds during their reproduction period. Here it may simply be mentioned that the sitting reaction in many birds seems to play the greatest part while the clutch is not yet hatched. Some species of birds, however, show a tendency to get off the nest in time before a disturber. The reaction of remaining on the nest is typical of *Galliformes* of northern Fennoscandia.

Without any connection with brooding activity, the reaction to remain on the ground as an answer to disturbances is found in many bird species under special conditions to be discussed here.

1. First we find that this behaviour is chosen by (a) small passerine birds living on the ground (*Oenanthe, Anthus, Motacilla,* [*Carduelis*], *Emberiza, Calcarius*), (b) some *waders* (*Charadrius, Gallinago, Lymnocryptes, Calidris alpina, Limicula, Phalaropus*), (c) some owls, especially *Asio flammeus,* (d) many ducks (*Anas,* excl. *A. platyrhynchos, Aythya ferina*), (e) *Rallus, Porzana, Crex.* As is easily seen, these groups have in common their adaptation to a life close to the ground.

2. We note that this behaviour is presented by the above-mentioned bird groups or species, when the birds act alone or in small flocks.

3. The birds usually remain on ground that is not unfamiliar to the species as to vegetation, texture or morphology.

4. Finally, we find that the behaviour of the disturbing animal (or man) is of a certain significance. If the disturber is an avian predator and is moving fast, rectilinear but not just in the direction of the sitting bird, then it is likely that the bird will remain sitting on the ground. As a matter of fact, a bird on the ground has quite often no chance to move elsewhere before a violently swooping *Falco peregrinus* has already passed by and is eliminated as a disturbance. An uncomplicated "escape *in situ*" as a simple reaction is, however, probably very rare (cf. TINBERGEN 1951).

(b) *Alighting on the ground or on the water*

1. *Normal alighting.* There is in many bird species a tendency to escape *into hiding* in vegetation, stones or other structures. Birds of the species mentioned in (a) above are likely to alight and hide on the ground. In special conditions other birds, too, may react in that way (RUDEBECK 1950 A, 1951). It is, however, a common misunderstanding that any bird would try to escape a peregrine falcon by alighting and that it would remain safe having done so. The kernel of truth lies in the fact that the motion curves of a hunting *F. peregrinus* and a crowd of birds are likely to be made in such a way that some birds will fall out of the dangerous zone and be able to hide on the ground or in the vegetation. Furthermore, some ducks, waders and passerine birds with a very narrow critical zone of disturbance will react by induction to the call and taking wing of birds which react with more sensitivity to the predator. If, then, the predator does not infringe upon the critical distance of the former birds, they are likely to alight very soon after moving a little in a random direction. In addition many a bird has "escaped" a *F. peregrinus* because the latter had *no desire* to hunt, having recently eaten, or just because such falcons may prefer to follow some other species.

Thus an alighting behaviour of a bird, although simultaneous with the appearance of a hunting predator, is not necessarily the adequate escape reaction to that predator.

2. *Alighting or diving into water as an escape reaction of waders, and perhaps of passerine birds.* Not seldom observations of waders (especially *Tringa*) escaping a predatory bird by diving into the water are recorded (cf. ESSING 1948, JENNING 1953). The present author, too, has a few observations of such diving behaviour in *Tringa*. Also CURRY-LINDAHL (*in litt.*) and RUDEBECK (verbal comm.) have had the same experience of *Tringa*. Pigeons, swallows and small passerine birds are mentioned also in this connection. Thus DURANGO (1948) tells of a *Columba palumbus* throwing itself into the water to escape a pursuing *Falco peregrinus*. In our attempts to find a probable interpretation, some observations have to be mentioned:

(1) The swooping variety of hunt may prove to be dangerous both to hunter and prey because of the moment of inertia in the downward accelerating motion curves of the birds involved. The author has thus observed accidents, where either the falcon or the prey or both have come to harm or have barely escaped a collision with trees, a wall or the ground.

(2) The swooping behaviour is obviously an innate reaction of falcons, in just the same way as the deviating behaviour is probably a true escape reaction of most passerine birds, whereas diving into water is not known as a true reaction in passerines.

(3) Diving into water probably does not play a great part in the fugitive behaviour of any passerine birds, since it would be difficult to learn.

(c)   The crowding behaviour

1. *Crowding in the air.* *Sturnus* and *Calidris* are often seen to be crowding very tightly, having taken wing at the approach of a predator. Sometimes the same behaviour is seen in *Plectrophenax* and more seldom in *Anas* or *Aythya* (cf. G. MARKGREN 1960). In order to escape, the birds then have to manœuvre simultaneously. (Very seldom the author has observed that behaviour also in *Gallinago*.) The predators avoid the crowd itself but are often seen to be hunting some bird lagging behind (RUDEBECK 1950 B, 1951, TINBERGEN 1951, CURRY-LINDAHL *in litt.*).

2. *Crowding in the water — swimming escape.* At Sjölunda, great flocks of *Aythya marila, A. fuligula* and *A. ferina* with some *Bucephala* and other ducks are every year seen to gather in shelter on the lee side of the quays during the winter. The number of birds may amount to about 10,000. When falcons or eagles are hunting in the locality, these ducks are found to be crowding tighter. The predators are never seen to make a real attack on these great flocks. If, however, an eagle is flying too close, the whole flock may swim slowly away from the eagle, and some proximal birds may dive or take wing and fly off to the distal side of the flock. At times lesser flocks of *Mergus merganser* behave in the same way. *M. albellus,* however, constituting flocks of about 100–300 birds at the most, are never seen to behave in this manner.

(d) *Slow swimming motions in water-birds*

Typical of the fugitive behaviour of the great crowds of ducks (except for *Anas*) that winter in Scania on the lakes is thus a series of reactions of low intensity, namely, in addition to crowding, a slow swimming movement away from the predator, sometimes with intention movements of rising or diving. In the extreme case the ducks may not even present any observable reactions to a *Haliaeetus albicilla* flying over them. Usually that "insouciance" towards predators is found only in great, well-crowded flocks, although it is now and then recorded in small concentrations of *Aythya*, *Somateria*, and especially *Mergus merganser* (MARKGREN 1959, ULFSTRAND 1960). This subject is to be treated by G. MARKGREN. Such lack of sensitivity is, however, sometimes obviously dangerous for the duck. As regards the interpretation of the swimming-escape behaviour, some circumstances have to be considered:

1. At a certain distance the observer may get a wrong idea of height, relative distance and direction of motions.

2. The predator, if it is a *Haliaeetus*, may be a fish specialist and perhaps personally well known to the ducks. Some *H. albicilla* fish in front of flocks of fishing *Mergus* and other ducks as a sort of "parasitism".

3. Anyhow, the behaviour in question gives an indication of a considerable lowering of the value of the critical distance for escape reactions in ducks in many cases. As this behaviour is obviously more common in small flocks of ducks on the Scanian lakes, where eagles and ducks winter, than at Sjölunda, where the eagles just come to hunt, and as it is never observed by the author in ducks on the lakes as a reaction to *the first eagles* of the autumn, experience is likely to play a part in the behaviour.

The swimming escape is also seen in *Gaviiformes* and *Podicipitiformes*. As was recently mentioned, the low intensity escape behaviour of swimming movements will, when the fugitive motivation is increased, change to more intense reactions such as rising or diving (cf. FABRICIUS 1951).

B. *Diving Escape in Water-birds*

Diving from the air or "pseudo-diving" behaviour in waders and passerine birds has been discussed.

The innate diving reaction is a common answer to a danger in swimming birds. A peculiar intention movement of diving ("sink reaction") is seen in *Podicipitiformes* and *Gaviiformes* and also in *Phalacrocorax* and *Anhinga* (K. CURRY-LINDAHL *in litt.*). These birds thus lower themselves until finally only the head and the neck reach over the surface. The next step is often real diving, and the whole escape pattern may be an alternate diving and swimming on the water surface. Notwithstanding this, a surprisingly rapid rising and taking-wing reaction can occur in *Gavia* if taken by surprise. The possibility of diving, or rather a potential conflict between impulses to dive and to take wing, may be one cause of many ducks

remaining on the water in fear. (See above on *Mergus* under (d).) The diving of water-birds is a well-defined behaviour, although it may consist of many elements of reaction (cf. TINBERGEN 1951).

C. *Running Escape*

Walking or jumping movements play a great part in bird locomotion both as intention movements and as locomotor elements. (For the discussion of locomotor movements, cf. DAANJE 1951.) Occasionally a bird with the habit of reacting to danger by sitting close may at first walk or run some steps before sitting on the ground. Especially in birds that do not jump but move by walking, the run will occur as an initial escape reaction. It is thus common in *Anthus, Motacilla, Alauda, Eremophila* and in many waders and game-birds, the escape of which may consist of alternate walking, running, sitting, and shorter or longer flights. This unspecialized (and primitive?) manner of escape is typical of *Lagopus lagopus* and *L. mutus* in early spring.

Running alone as an entire escape reaction is not found in any Fennoscandian bird species.

D. *Fast Swimming Escape—Running on the Water*

The fast swimming behaviour shown by the clutch of a water-fowl such as *Mergus* is just a sort of run on the water. Also in *Gavia, Podiceps* and *Cygnus* fast swimming and running on the water is of a certain importance in escape and will occur both as independent fugitive behaviour and as an intermediate link between swimming escape of low intensity and the escape reaction of taking wing. The wings take part in the behaviour both as carrying planes and by way of a spring function (DAANJE 1951). At least in *Mergus serrator* the running on the water reaction is innate. Whereas the combination of running on the water and taking off for flight is found in the birds just mentioned and is also typical of other ducks such as *Aythya* and is common in *Alcae*, the hop initiates the taking wing of *Anas* species and of *Cinclus*.

When the fugitive motivation is high and the disturber has approached too close, then the typical escape reaction of probably any bird with carrying wings is just the avian behaviour par préférence of taking wing.

E. *The Taking-Wing Reaction*

(a) *Definition and characteristics of the behaviour*

The author has for about 15 years taken an interest in taking-wing behaviour as regards both its locomotor function and its significance in bird behaviour. Here it will be treated only from the point of view of fugitive behaviour. Taking off or taking wing (in Swedish, uppflog) is an outstanding behaviour, well defined as the locomotor momentum of *initial flight*, i.e. the moment when sitting or locomotion on ground or water is changed into locomotion in the air by the carrying

function of the wings. Although in the bird there may be a gliding scale of motivational intensity throughout the fugitive behaviour pattern as revealed by slight indications of intention movements or by bodily escape, yet in the locomotor performance there is in the taking-wing momentum (the "uppflog"), as regards both the mechanical principles and the locomotor anatomy of the bird, something new in principle. It is thus not to be compared with the hind-leg locomotion of swimming, walking or running of different intensities, since only in flight are the avian arms taken into use in their typical avian function as wings.

It is from that point of view that the author has laid stress on the "uppflog", the "fly up" moment as a manifestation of an intra- and interspecific comparable physiological and mechanical performance, regardless of the psychological tension of the bird. The exact amount of energy applied in the action could be measured and compared by physiological methods, though this has not been done by the author.

(b) *Intention movements*

Fortunately, the *intention movements*, too, that may precede the "fly up" in a bird's taking wing are easily observable (Daanje 1951). In the intention movements, legs and wings as well as head and neck are unmistakably engaged. For comparison it is thus possible to distinguish between (1) birds presenting no observable reaction, (2) birds showing indications of being disturbed, and (3) birds reacting with "uppflog", thus taking wing as an answer to the disturbance. If the birds then go on with escape flight or do something else, is partly a question of complicated interaction, as will be seen below.

(c) *Relation to flying*

The Swedish ethologist Fabricius (1950 B) has found in experiments with young gulls and terns, that the flying behaviour of these birds is developed before the birds are able to manage to take wing or to alight. He writes (op. cit.; the original is in Swedish): "In young gulls and terns the author has proved that the instinct actions, which make possible the real flying, are entirely developed earlier than the reactions that are connected with the starting and the landing." Fabricius tells that a young gull at a certain stage of development, when thrown up in the air, will fly with considerable ability for a time; growing tired, however, it will make an unsuccessful landing. Some days later the "instinct" of starting, of taking wing, will awake spontaneously. This statement is of interest in the present discussion. It indicates that the nervous controls or the "neural organs" of the taking-wing reaction possess some degree of independence in the great reaction complex of flying behaviour.

(d) *The distribution of the reaction in species and its occurrence in different situations*

As a matter of fact, the "uppflog", the reaction to take wing at a disturbance is found in all bird species that the author has yet had the opportunity to study from

that point of view, i.e. most Fennoscandian birds and some species of S. and W. Europe.

This reaction will be seen as the answer to an approaching man, to avian or mammal predators or reptiles, to acoustic disturbances and to different artificial disturbances. It will be found as the spontaneous reaction to *Buteo*, *Aquila* or *Haliaeetus* as well as to *Falco peregrinus*.

The critical distance will be much different in different species and in varying situations. Some birds at first will sit close (*Gallinago*, for instance), other birds will run a considerable distance before they eventually take wing, for example, *Otis*. Many small passerine birds take wing at the approach of a predatory bird only if it comes very close. The author would suggest that this behaviour will not be entirely lacking in any bird species as a reaction to animal disturbers at a certain critical distance, providing the bird has carrying wings.

(e) *Reduction and inhibition of escape*

Whether the reaction to fly up for a danger be entirely innate, which is probable, or whether it be to some extent a result of "learning" during the very early days of a young bird's life, which is less probable, it has to undergo a certain development as behaviour and has to be perfected by experience. In the further development of the bird the perfection of inhibition mechanisms is of great value. Here the animal as well as the non-animal environment will play a part, as will be discussed.

Of interest to our subject is to what degree escape reactions can be inhibited and how that is done. On the other hand, we have to consider the role of experience or "learning" in reducing the fugitive reactions. It has already been mentioned that the birds of Sjölunda (with the exception of the great crowds of *Aythya* and some other ducks) react sensitively to any predatory birds. It was mentioned, too, that ducks and many other birds react with less sensitivity to birds of prey on the Scanian lakes during winter. The problem is discussed to some extent. Often it will also be heard that birds react in one way to *Accipiter nisus* and *A. gentilis*, in another way to *Aquila* and *Haliaeetus* and finally again in some other manner to *Falco peregrinus*. Although the interaction between predators and prey has to be treated below, we have to consider some circumstances here.

1. At a place where many species of predatory birds are frequently on the hunt, a standard escape behaviour of "running no risk" would be likely to occur. As will be seen from the tables, Sjölunda is just such a place (Tables I II). There the standard reaction to peregrine falcons as well as to eagles is taking wing, both in gulls and crows.

2. At a place where avian predators of different species have for a long time "lived together with" the presumptive prey, the latter will *adapt themselves* to the predators *with sensitivity* as regards the actual danger and the specialisation of the birds of prey. The Scanian lakes are localities of that kind. Of course, some bird or other makes its last and fatal mistake by inhibiting the escape.

3. In an area where few predatory species hunt, perhaps only *Falco peregrinus* and *Accipiter gentilis*, and where the former species hunts by swoops, whereas the latter does not, and where the peregrine does not hunt crows as a rule, there the crows will perhaps not take wing for a peregrine. Such a place is, however, not known to the author.

F. *The Mobbing Behaviour*

(a) *Introductory*

Whereas in the previously discussed examples of avian reactions to predators and other disturbances the behaviour has been characterized as either obviously *fugitive* or as (seemingly) non-fugitive, some other behaviour elements to be treated below are clearly distinguishable as *hostile*. In the present chapter we meet with an activity of the bird that is *both fugitive and hostile* at once, the mobbing reaction.

(b) *Definitions and characteristics*

Although the behaviour in question has long been known by the naturalists, a concise definition was given first in the important paper on interspecific recognition by HARTLEY (1950): "A mobbing is a demonstration made by a bird against a potential or supposed enemy belonging to another and more powerful species; it is initiated by the member of the weaker species, and is not a reaction to an attack upon the person, mate, nest, eggs or young of the bird which begins it. In this definition stress is laid upon the fact that a mobbing is not provoked by hostile actions. It is a reaction to a dangerous aspect." As a complement to this definition, some more lines from HARTLEY (1950) are also quoted:

The reactions of small birds to the appearance or discovery of a predator are several. They may take refuge in flight or cover, sometimes accompanying or following the reaction with "alarm" cries; by gesture, voice or bearing they may exhibit uneasiness or vigilance, without seeking refuge; they may (seemingly) ignore the predator; or they may mob it. In a mobbing the predator is approached by one or more birds, which follow or circle it with outcry and gesticulation each after its kind, until the object of the attack departs or until its persecutors presently move away to other activities. Mobbing behaviour is to be distinguished from aposematic or pseudaposematic displays undertaken defensively, and from "diversionary displays" (Armstrong 1949) in that a mobbing is not a reaction to an actual attack by the enemy. It is not proposed here to discuss the possible survival value of the mobbing habit. This survival value is obscure, for often the predator seems to be in no way disconcerted by the demonstrations. Occasionally, mobbing behaviour seems to be positively disgenic, for there are records of an attacking bird being killed in the assault (MASON 1915, RYVES 1942, BROWN 1947).

TINBERGEN (1953) has also pointed out that the mobbing or rather the alarm calls of mobbing are "a clear example of an activity which serves the group but endangers the individual. Such social attacks have various functions. If the predator is only moderately hungry, it can often be seen to hurry away as soon as the attack develops. When a Sparrow Hawk is really hungry, that is, when it is

hunting intensively, mobbing does not disturb it much. It nevertheless distracts part of its attention from detecting other prey." In a valuable contribution to the dicussion of our subject ALTMANN (1956) concludes: "In the presence of a predator, a bird may do one of several things. It may fly into dense foliage or fly away. It may remain within sight of the predator, but indicate by its voice or actions that it has recognized a foreign object in its environment. It may not respond to the predator at all. It may attack the predator. The first three types of reactions are not restricted to predators, but are the typical responses of birds to a wide variety of objects. In contrast, the attacks of birds known as "mobbing behaviour" are almost entirely restricted to natural enemies or to stimuli resembling them." We shall return to the definitions later on.

(c) Interspecific differences

ALTMANN (1956) points out that *species* "differ in their mobbing behaviour patterns, even in response to the same species of predators". Of great interest to our subject are the concentrated descriptions of the mobbing behaviour in some passerine birds in response to stuffed specimens of screech owls (*Otus asio*), especially that of *Calypte anna*. The interspecific differences, however, are to a certain degree dependent on general habits and locomotor patterns of the species. Thus the behaviour of a mobbing *Troglodytes troglodytes* or a *Regulus regulus* will as a rule consist merely of yellings from hidden positions, whereas the mobbing by a *Hirundo rustica* or a *Motacilla alba*, *M. cinerea* or *M. flava* is likely to be performed as a swooping attack, regardless of whether the object of the mobbing be a cat, an owl or a hawk. Also the mobbing "attack" by a *Larus canus* will be, regardless of the intruder, both less noisy and not so dramatic as that performed by a *L. ridibundus*, a *Stercorarius longicaudus* or a *Hydroprogne*.

Here we should mention something about the distribution of the behaviour, too, as regards species and individuals. To some extent this behaviour is found in some variety in most Fennoscandian bird species observed by the author (for exceptions, see the summary). We may thus conclude that mobbing is a common phenomenon. No less important is the fact that the behaviour may be presented to predators and non-predators of (almost) any species. In the tables of the present paper will be found examples of mobbing against predatory birds (1) while they are *hunting*, (2) when they are *resting* after hunting or between attacks, (3) when they are *going away* with prey, or (4) are engaged in *eating* recently captured prey. The tables, however, only consist of those instances in which the predator was also seen *hunting* but not the observations of birds of prey eating or resting and then being the object of mobbing birds, unless it later on made an attack on the mobbers. Neither has the author found it possible to make a list of the observations of birds mobbing *non-predators*. The reason is not merely a desire to limit the extent of the tables but also a desire to complete the material on questions such as, for instance, the problem of seasonal variations in the fugitive behaviour.

(*d*) *Seasonal differences*

ALTMANN (1956) found seasonal changes both in the number of birds mobbing a predator and in the duration of mobbing. There are clear maxima in May and June in the ratio of "Bird-minutes of reaction/minutes of trial", i.e. "the sum of the number of minutes that each bird reacted divided by the number of minutes involved in the experiment." Other less outstanding but not less interesting maxima are found in January and December. The ratio of "Bird-minutes of reaction/minutes of trial" were for May 1.90, for June 4.40, for August 0.00, January 0.224 and for December 0.759 (op. cit., p. 243).

(*e*) *Mobbing reactions in general*

The author has laid stress above on the interspecific differences in mobbing birds' behaviour regardless of the species of predator. The intraspecific variety is mentioned too. But to what extent is there a "recognition" of different species of predators? It is generally accepted that a mated bird knows its partner and is able to distinguish it at a great distance, even among members of the same species (LORENZ 1931, ROSENBERG 1934, LACK 1943, TINBERGEN 1951, 1953, 1958). Nevertheless there are indications that there is no unity and identity in the objects of the perception of a bird. This seeming contradiction is explained by the limitation of the avian perceptual mechanism, which works with isolated features of the objects, some of which are more important than others, and to which the bird will react. From these reactions to special features, releasers or signals (TINBERGEN 1948, 1951, 1958), it may seem sometimes as if the bird made mistakes and was not able to distinguish between dangerous and harmless objects, whereas in other respects the "recognition" and the behaviour seem almost perfect. Now in our observation and discussion of behaviour we might conclude that actions obeying rigid patterns are due to innate mechanisms, whereas seemingly pliable behaviour is likely to be put down as probably due to "learning". A related possible error is to describe and discuss uncomplicated reactions but overlook more complicated behaviour and series of reactions. Probably many important problems of mobbing behaviour are to be solved by study of the reactions of birds raised in isolation.

Reactions to owls have caused the greatest interest, mostly in the discussion of mobbing behaviour. Some features of the mobbing behaviour, however, could be obtained from the study of avian mobbing as a reaction to other predators and non-predators. For the sake of brevity the author will confine this discussion to some few species common at Sjölunda and, as to one species, in some cultivated areas.

(*f*) *Mobbing behaviour to members of Strigiformes*

ASIO OTUS. The long-eared owl has as a rule been perched on a branch of some dense coniferous tree (*Picea*, *Abies* or very often *Thuja*). When mobbed or disturbed

by man, the owls have flown from one tree to another remote or denser tree, often a *Thuja*. Rarely have the owls taken to soaring. The observations were made during the period January March in 16 winters. The mobbing birds were *Corvus corone cornix*, *Pica pica* (*Garrulus glandarius*, *Corvus monedula*), and *Larus argentatus* (*L. ridibundus*). The *progress of mobbing* has nearly always been the following:

(1) The owl(s) is discovered by a magpie, a crow or a jay, usually by a magpie.

(2) The magpie immediately starts screaming and takes a position in a tree quite close to the owls or at the top of the tree where the owls are sitting.

(3) More magpies (and crows) join in quite soon.

(4) Some of the magpies are silent or call only occasionally. Other birds scream all the time. Some few magpies circle around the owls' tree, occasionally swooping at the tree.

(5) The owls or some of them now leave the tree. (Crows or jackdaws may join in mobbing.)

(6) Magpies are seen pursuing the owl, screaming and occasionally with a sort of swoop.

(7) The owl perches in a new *Thuja*.

(8) As before, from (2) to (5), until finally the owl manages to hide itself.

(9) In some few instances the owl will go on soaring or flying at a considerable height.

(10) On these occasions crows or herring gulls will be seen circling around with the owl in behaviour identical to that towards a short-eared owl. Crows and jackdows are most interested in flying owls, whereas the jay will take part in mobbing just by screaming, whenever it comes across a mobbing group.

ASIO FLAMMEUS. This species is found resting on the ground in dense herbage. If disturbed, the owls fly off one by one in different directions; some of them may hide in the herbage somewhere, thus escaping the mobbing crows or gulls. Quite often this owl will go on soaring for some minutes or an hour. The mobbing birds are the same as those mobbing *A. otus* except for *Garrulus* and with the addition of *Accipiter nisus* and some small passerine birds.

(1) The owl may be discovered by a gull or a crow, seldom by a magpie.

(2) As soon as the crow starts screaming or the gull makes a (harmless) swoop, the owl will take wing.

(3) Often the owl itself initiates the events by flying out over the gulls and crows causing the escape reaction of taking wing.

(4) As the owl begins to fly with its typical deep and high wing beats or goes over to soaring, the gulls and/or the crows alight, except for some few individuals, who will go on for tens of minutes, circling about with the owl in a harmless sort of mobbing. Magpies play little part in mobbing of this owl with its habit of moving in free air.

The observations were made in the period (December)January–April(May) over 14 years.

STRIX ALUCO. The observations were made occasionally. Here the mobbing birds were *Corvus corone cornix*, *C. frugilegus*, *C. monedula*, *Pica*, *Garrulus*, and small passerine birds. No real attacks or swoops were observed. It seems as if *Strix aluco* is somewhat less disinclined to fly away than the above-mentioned *Asio* species.

SURNIA ULULA, GLAUCIDIUM PASSERINUM, AEGOLIUS FUNEREUS and ATHENE NOCTUA. Occasionally the author has observed passerine birds mobbing these species. As, however, the total number of observations is small (about 80) and the observed behaviour pattern is not uniform, the matter has to be reserved for completion. Only one conclusion may be drawn from the material mentioned, namely, that any owl of the four species in question that flies away from its mobbers is likely to be the subject of swooping attacks by many small bird species, just like an "escaping" *Accipiter nisus*.

(g) *Mobbing behaviour to members of Falconiformes*

Most observations were done in the winter over a period of 16–18 years.

FALCO PEREGRINUS. This predator is often the object of mobbing by various species. All the aforementioned species but seldom *Pica*, *Larus argentatus*, *L. marinus*, *L. fuscus*, *L. canus* , and *L. ridibundus*, are common mobbers of this falcon, as is *Vanellus vanellus*. Also birds of prey will occasionally be involved in the mobbing of a peregrine. Thus the following predatory birds are recorded in this behaviour: *Falco columbarius*, *F. tinnunculus*, *Accipiter nisus*, *Buteo buteo*, and *Pandion haliaetus* (!)

The following outline of events in the mobbing of a peregrine falcon, *mutatis mutandis*, may also represent the mobbing of a *Falco rusticolus*:

(1) The falcon is hunting and all the birds, except the swans, are on the wing for escape at the initial moment.

(2) The falcon is swooping at a crow or a herring gull but in vain.

(3) As the predator goes on looking out for new objects for its hunt, the crow or gull recently chased or some other crow or gull in the neighbourhood will follow the falcon with repeated swoopings or just follow screaming continually. Lapwings are "attacking" the place where the falcon was recently or some harmless bird.

(4) Now the falcon will *turn round and hit* at the mobber or try to clutch it with his claws. A gull may be struck without being killed.

(5) The predator may go down to the ground or ice for a rest.

(6) Here a lot of bird species will come to pay their reverences by calling, striking at a distance of some tens of meters or taking a position some hundreds of meters from the falcon.

(7) If the falcon rests for a long time, an hour or more, the mobbing will cease.

(8) When the predator takes wing, events will run, as mentioned, from (1) and so on.

(9) Sometimes the falcon is seen to capture a prey. In flying away with the quarry, it will be the object of mobbing, especially by crows, herring gulls, black-headed gulls and other predators.

(10) If the falcon alights on the ice to eat the prey, it is constantly attacked by crows and/or gulls more or less violently.

(11) Sometimes the crows approach, at first flying and calling, then on foot, growing almost silent as if they were waiting for the remains of the prey. They may thus come quite close, some few meters from the peregrine.

(12) One or other of the crows, however, will make an attack or get too close and will then be chased away.

(13) At that instant a general screaming and mobbing will begin after an escape flight by the entire company. ((11)–(12) may be repeated.)

(14) The falcon may leave its prey too long, just long enough for a crow or a herring gull to rob him of it.

(15) Quite often the author has detected the peregrine with its prey and the mobbing crows or gulls without having witnessed the preceding hunt. In approaching then—as a rule on the ice—the critical distance for reaction to man has been reduced in the crows or gulls, the falcon being the first to react by escaping from the author. These occasions are not listed in the tables.

FALCO COLUMBARIUS, FALCO TINNUNUCULUS, ACCIPITER NISUS. In the avian mobbing of little falcons or hawks the species recently mentioned as mobbers of *Falco peregrinus* are involved and besides waders, small passerine birds and birds of prey. But there are still more differences.

(1) The attacks on a little falcon or a sparrow-hawk are more like a real attack than what is seen in the "swoops" on a peregrine falcon.

(2) These little falcons and the hawk, whether they are on the hunt or have captured a prey, are likely to escape when mobbed by crows or gulls.

(3) Magpies here play a great part in the mobbing as in the mobbing of owls.

(4) The little falcons and the sparrow-hawk are seen mobbing each other. Also *Buteo buteo* may be involved.

(5) As regards the kestrel, it will be mobbed by crows or gulls when hunting in the fashion of a merlin or a hawk, but hardly in its hovering hunt.

AQUILA CHRYSAËTOS, AQUILA SP., AQUILA CLANGA and HALIAEETUS ALBICILLA. The group of great eagles has to be treated as a unit in this connection for reasons that will be given below.

Corvus, excl. *C. corone* and *Larus*, excl. *L. minutus*, are frequently involved in mobbing attacks on eagles. The same is to be said of birds of prey of any species found simultaneously with eagles in Scania. In addition the same birds are seen mobbing eagles as are mentioned above in the mobbing of owls. Geese or ducks are, however, not seen mobbing eagles. Thus, the eagles are attacked by those bird species that they usually do not prey upon, whereas their presumptive quarry species do not mob. Some important features must be mentioned:

(1) Just as in the famous swoopings of *Falco rusticolus* and *F. peregrinus*, no bird is seen to attack at the moment of an eagle's powerful pouncing or swooping, whereas, for instance, a crow may attack a swooping sparrow-hawk.

(2) Eagles carrying prey or eating it are attacked by crows, magpies, or lesser predators in an almost incredible way, while the eagle—irrespective of species in our group—shows just as incredible ignorance of the mobbing birds.

(3) Flying and especially *soaring* eagles are mobbed for hours by crows, gulls and/or other predatory birds.

(4) The soaring eagles when mobbed are more seldom seen to attack in response to the mobbing birds. Here *Aquila* and especially *A. clanga* react more sensitively to mobbing than the sea eagle.

(5) Perched golden eagles and sea eagles are often mobbed by crows or predatory birds, sometimes also by herons (*Ardea cinerea*).

(6) Eagles "mob" each other intra- and interspecifically. There is a common idea that eagles are somewhat playful to each other. The limit between frolicsome and hostile activity, is, however, not always so clear. Fear and escape may also easily come into the picture quite obviously. Thus two eagles of the same species (*Aquila chrysaëtos* or *Haliaeetus*) may be seen to chase each other alternately from a place on a branch of a tree or some other high position. The behaviour may be interpreted as a sort of fight for a favourable place. It is perhaps not to be described in terms of display, nor perhaps in terms of mobbing. But if an *Aquila clanga* meets an *A. chrysaëtos* or a *Haliaeetus* in the air and they then enter upon swooping and clawing at each other, is then the spotted eagle *playing* with, *fighting* with or *mobbing* the bigger eagle?

(h) *Mobbing behaviour directed against non-predators*

Especially in March–May some non-predators become the objects of mobbing.

ARDEA CINEREA. Crows, gulls and waders are seen to attack herons in flight or on the ground in the same manner as they mob eagles.

CORVUS CORONE CORNIX. The crows are mobbed by gulls, waders and passerine birds also without any observable connection with territory or nest.

LARUS ARGENTATUS. The herring gull is mobbed by crows and by *Larus canus* and *L. ridibundus* in the same way as the crow is attacked. The behaviour may be recorded far outside the territory and long before breeding, although it is more frequent and more pronounced when the nest and the eggs are in danger. Finally here must be mentioned very peculiar behaviour noted in *Vanellus vanellus*. At Sjölunda the author has in not a few instances seen a lapwing fly out of its territory in the direction of a herring gull at a considerable distance and begin to attack it. One spring the author had to pass about 200 m from the nest of a lapwing each morning when making his way along the foot of a fence. The lapwing would come each morning to mob the author and, funnily enough, when the nest was already out

of sight. The bird would follow him almost to the railway station, more than one km from the territory, mobbing all the time.

(i) Summary and conclusions

1. The "mobbing behaviour" is a common but not a general avian behaviour.

2. The run of events in mobbing will show intraspecific and interspecific differences. There are also differences in the behaviour towards various objects.

3. "There is a *vernal increase* in the number of birds that 'mob'" (ALTMANN 1956).

4. The behaviour is defined by HARTLEY (1950) as "a demonstration made by a bird against a potential or supposed enemy belonging to another and more powerful species". It may, however, be shown towards equal or even inferior birds too.

5. Fugitive reactions and reactions of hostility are simultaneous constituents of mobbing.

6. Traces or interferences of other "interests" or complexes of activity are seen in avian mobbing; thus, for instance, looking out for, or even fighting for, food. The vernal maximum may have a bearing on the reproduction complex.

7. The attributes of "superior, equal or inferior" are not constant qualities of a bird but merely changeable characters in the mutual interaction of birds. Thus, a bird that from our point of view is "more powerful" than another bird may, owing to its behaviour, be "inferior" to that bird in an actual relation of reactions. A bird that is the *object* of mobbing is at that instant inferior to the mobbing bird in the relationship of mobbing. As is seen above, however, the roles will shift to and fro. And in the mobbing bird the inclination to escape will alternately be stronger and weaker than the urge of hostility just as the behaviour is seen to be changing.

8. In the discussion of whether mobbing is innate or not, it must be considered that the mobbing behaviour is not merely one reaction but the result of a complicated interaction of impulses and that experience anyway will play a part in it. As we do not know how much is innate, we must first describe the behaviour of mobbing not in terms of releasers but in quite neutral terms of behaviour.

Obviously the behaviour of the object of mobbing is of major importance to the mobber. A bird is likely to be mobbed in the following situations; (a) in flight directed away from the mobbing bird, the moment of motion immediately after an unsuccessful swoop being a special occasion; (b) if the bird in question has captured prey and is carrying it; (c) in eating the quarry; (d) in sitting.

(j) Discussion of experiments

In most European countries it has long been known that a stuffed specimen of an owl will allure passerine birds to crowd in order to attack the owl. The mobbing birds thus have been shot or trapped in some way by hunters. (Living owls have also been used.) These hunts with stuffed owls or wooden dummies are the first

known experiments in avian mobbing. Modern experiments have proved that "perched" wooden dummies are as useful objects of mobbing as stuffed specimens, if they are, within a considerable range of size, (1) owl-like in outline, (2) solid in contours (or solid-looking by shading), (3) coloured in browns and/or greys, (4) patterned (HARTLEY 1950).

These valuable field experiments by HARTLEY complete our field experiences of mobbing birds with some concrete answers to the question, what kind of sedentary phenomena do wild birds in the field mob on certain occasions? The question of mobbing sitting predators is very suitable for experiments. As regards the question of innate or not, no answer is, however, given by the above-mentioned experiments. On the other hand, some experiments have been made with hand-reared birds, the result of which is a high degree of probability that reactions of fear and escape towards models characterized by the same qualities of size, shape, coloration or tone as in the experiments just mentioned are innate fugitive reactions. And that is of importance. Obviously the mobbing behaviour shown by passerine birds and gulls towards flying predatory birds and predators with prey has to be regarded as the same behaviour as the "demonstrations" by passerine birds against a sedentary enemy. The mobbing behaviour shown by wild birds in the field should be regarded as one of many possible reactions in which fear and hostility are involved, and the one in which the opposed urges of hostility and escape almost balance each other.

G. *Fighting in Defence*

As is mentioned above, hostility is present in many fugitive reactions; sometimes there is a balanced interaction between escape and aversion, as in the mobbing behaviour recently discussed. It is occasionally found that mobbing is succeeded by a real attack on the predator or the predatory model (ALTMANN 1956). Thus the dummy may be of a "too sedentary behaviour". On the other hand, the fighting may take the form of competition for food, when the predator is about to eat captured prey. (There will always be *something* left for the crows or gulls, if the predator does not fly away with the quarry.) On some occasions a sort of mutual mobbing will occur.

"*Fighting in defence*" here, however, means something different from merely occasional demonstrations of hostility. It means anything from the utmost struggle to get free of the killing claws of the predatory bird to the pronounced counter-attack, when the bird or its offspring is in danger. There is clear evidence to be obtained in the field that such fighting by an "inferior" bird will occasionally save the fighting individual or its young from an attacking predator (RUDEBECK 1950 B, 1951, MARKGREN 1951, 1959). SMITH (1958) tells of a winged *Anser fabalis* not only defending itself with bill and wing successfully against four *Haliaeetus albicilla* but also making repeated attacks on an eagle standing on the ice, with the result that the eagle moved away. Fighting is likely to occur when the attack of the

predator is directed against (1) the young or the brooding mate of a bird, (2) a hurt bird or a bird that is in some way not able to fly, (3) a bird that is caught or is about to be captured. The intensity of the fighting depends on the ability of the birds, if the one be in some way superior to the other.

H. *Escape by Personal Withdrawal ex loco*

Both in hiding and sitting close, in mobbing and in defensive fighting, the bird's behaviour is to a great extent an *escape in loco*. There are, however, possible escape reactions in which spatial locomotion plays a considerable part, i.e. in the *escape flight* before a hunting predator. This subject will be treated in Chapter V, as there is in such escape behaviour a certain aspect of *interaction* between hunter and prey that demands a special discussion. Escape from a predator or some other disturbance by *personal withdrawal ex loco* is a common avian behaviour during migration or wintering and consequently a less frequent behaviour in the reproduction period. It is also typical of swallows and swifts in their breeding season, probably because flying is such a common reaction in these birds. There are certain interspecific differences in this behaviour also during migration and wintering of the birds.

Corvus corone cornix is thus seldom seen to react in this way, whereas *C. monedula* often and *C. frugilegus* not seldom will escape *ex loco* from a predator, even when not hunted. It is also quite obvious from the material the author has collected that *single birds*, and especially birds with social habits, will react to a predator by direct escape out of the place. During the migratory period of a species, the escape reaction in question is seen to be succeeded by migration flight, especially in *favourable weather* (see above). The behaviour in winter is often the initiation of the migration to a foraging locality. It is thus sometimes difficult to draw a limit between extended escape and migratory behaviour initiated by escape reaction. Migration at Ottenby initiated by shots is mentioned by EDELSTAM & RAMEL (1956). It is also often experienced at Falsterbo, when ducks or pigeons and doves are hunted. In the Congo flocks of *Motacilla flava* were often induced to migrate by shots (K. CURRY-LINDAHL 1953, 1954, 1958).

In the reactions of birds there will seldom occur a reaction *in absurdum*. From that point of view it would be of interest to study the further development of the personal withdrawal *ex loco*, when there is no persecuting predator. Such a study, however, is seldom possible except under special conditions, such as obtain in high mountains in cold air with excellent visibility. The author has had the opportunity to make some few field observations of such extended escape flights. They seem to occur very seldom.

Before dealing with the interaction between *hunting and escaping* we will discuss the *spatial arrangement* of the directed fugitive reactions in their development from non-directed initial taking-wing to the activity intermediate between behaviour *in loco* and pronounced activity *ex loco*.

2. **Spatial Patterns in Initial Moments of Fugitive Motion**

A. *Definition and Introduction*

The concept of "spatial pattern" is here used for avian motion curves in space, frequently observed in the fugitive movements of flocks or crowds of birds. According to the definition, the discussion has to be based on the presence of considerable numbers of birds. In order to give the reader a clear idea of the magnitude of the material for observation at Sjölunda, a few figures will be mentioned. The bird frequency at Sjölunda and Löddeå is treated by the author both from a faunistic point of view and from the migratory aspect. The ratio of the number of birds (of a species) to the number of days with more than one bird (of that species) observed has for species that are not merely accidental reached values from two to four figures. And the absolute maximum number of birds observable at one time is thus often of considerable value, as will be seen in a few examples: *Corvus corone cornix* 1100, *Fringilla montifringilla* (with elements of *F. coelebs*, *Emberiza* and *Chloris*) 4000, *Larus argentatus* 22,000, *L. ridibundus* 3000, *Charadrius apricarius* 8000, (1951) *Vanellus vanellus* 6000.

It has happened that about 40,000 birds have been on the wing simultaneously, all of them reacting to the same disturbance, a shot or a hunting bird of prey. Now, the motion curves of the reacting birds will be to some extent dependent on the sort of disturbance in action. There are, however, also interspecific differences bearing on the *habits* of the reacting birds. The *structure* of *the locality* will also play a part in the weaving of the pattern in question. *The dependence on the nature of the disturbance* is shown by the reaction to a shot. The birds are not able to localize the disturbance in the case of one single shot. All the birds take wing, calling and flying about. Some birds leave the place, whereas the majority in time return to their earlier positions. When, on the other hand, steam is blown off from the power station at Malmö with much noise for a long time, the gulls always move in a direction away from the station. That disturbance, as well as the shooting, is common at Sjölunda with its two shooting-ranges.

The dependence on *the locality* is clearly demonstrated in the compulsion of water-birds to water, whether it be the sea or a lake or a narrow brook to which the birds "want" to return after an alarm reaction. Ducks that have been disturbed on the surface of a lake are very likely to fly around the lake. This behaviour is often found also in other birds and is here called "circular flight". Such activity will be difficult to carry out over a brook, where the behaviour may be modified into a flight along an elliptic curve. At the seashore, water-birds are often seen to escape into the water when disturbed by a predator moving along the shore or by a man walking slowly. At the same time the *Numenius* species are likely to escape into the meadows as are also *Charadrius apricarius*, *C. squatarola* and *C. morinellus*, whereas *C. hiaticula*, *Limosa lapponica* and all the *Calidris* species observed will be confined to the very shore, as are the gulls with the exception of *Larus minutus*, which will often move landward to escape.

Crows taking wing for a passing peregrine in the typical vertical flock.

The above-mentioned instances are good examples of how the fugitive reactions are influenced by the habits of a bird, i.e. the differences are of an *ecological* nature. The same can be said of the behaviour shown by some species living in the boreal forest, or the taiga, such as *Pica pica, Nucifraga caryocatactes macrorhynchos, Perisoreus infaustus, Bombycilla garrulus, Pinicola* and *Loxia*. These birds will make a real dive into the base of the tree, when they are disturbed by a predator, thus trying to escape in the vegetation near the ground. There are, however, also interspecific differences, the explanation of which is not obvious. The *Galliformes* show, for instance, some interesting differences in their flying escape. *Tetrao* and *Tetrastes* are found to move below the concealing branches in escaping, a behaviour also found in *Lyrurus* and *Lagopus lagopus*. These are, however, not seldom seen to reach a considerable height during their flight (cf. the behaviour of disturbed *Phasianus colchicus*).

The above-mentioned interspecific differences of fugitive behaviour cause a sort of pattern in a reacting crowd consisting of many bird species. But patterns of another order are found in escape reactions, as will be shown. To begin with, a behaviour of the crow, when disturbed by predators such as eagles or falcons, will be treated.

B. *Crowding into Sparse Flocks after Taking Wing*

When a locality is struck by the sudden appearance of a *Haliaeetus* or a *Falco peregrinus* (or *F. rusticolus*), there is, as often mentioned already, a general taking-wing reaction from the birds, except for some small birds such as finches, larks and so on. Quite soon the behaviour will run on well-defined lines for most species,

Ducks in circular flight for a kite.

if the predator is not going to hunt about in the flush. Most jackdaws are likely to withdraw *ex loco* immediately. Not so the crows. Their number often amounts to some hundreds but seldom to more than a thousand. They crowd into sparse flocks, sometimes only one great flock, where the motion is greatest in the vertical direction. Nearly the same pattern is observed in *Corvus corax* on a few occasions. The behaviour is seldom seen in pure flocks of *C. frugilegus* at Sjölunda. In Lund, where many jackdaws winter, the author has on eight occasions seen these birds behave in a similar way. The crowds of Sjölunda crows are not seldom mixed with a few jackdaws or rooks.

On the European continent the behaviour described seems to be unknown. There, according to the literature, the crows *sit close* for a hunting peregrine falcon (TINBERGEN 1951). This behaviour of the crow has, however, never been observed by the author in Scania or elsewhere in Fennoscandia as a reaction of crows to the peregrine. For that reason it would be of interest to get some facts about the circumstances of any observation of crows remaining *in situ* or alighting for *Falco peregrinus* or *F. rusticolus*, such as, for example, (1) detailed notes on the behaviour of the falcon, including a description of motion curve and height at its passing over the bird(s) in question, (2) if possible, a description of a projection in the plane of the motion curve in relation to the "prey" with the distances computed, (3) detailed notes on the behaviour of the crow(s), (4) a description of the place, its vegetation, and surveyability, and (5) the meteorological conditions at the time, including the visibility. The question will be discussed from the aspect of interaction below.

C. *Radiating Pattern of Flight*

If a falcon makes an almost vertical swoop or if it rises in a steep curve from the ground or if a predator eating a captured prey all of a sudden takes off, then the birds in the neighbourhood will quickly take wing and evacuate the neighborhood of the predator. In a great crowd of birds, especially gulls and crows, the reaction will propagate like a wave, thus causing a movement of the entire crowd in a random radial direction outwards from the predator as the centre. Perhaps of most interest is the propagation wave indicating a *secondary, induced reaction* (TINBERGEN 1951).

The behaviour has been noted as reaction to *Asio flammeus* taking wing, *Circus cyaneus* ad. ♂ taking wing and often as reaction to *Falco peregrinus*, *F. columbarius*, *F. rusticolus* in swooping. It was seen as reaction to *F. peregrinus*, *Aquila chrysaëtos*, *A. clanga* and *Haliaeetus* flying off from a quarry and twice to *Aquila clanga* swooping down. The reacting birds have mainly been *Corvus corone cornix*, *Larus argentatus*, *L. ridibundus* and *Pica* in primary reaction. Other birds have obviously reacted by induction. This behaviour is explained as an evacuation of a dangerous zone, the random outward directions of the flying birds being transformed into a radial pattern by interaction of the reacting birds of the crowd.

D. *Circular Flight*

In Sections B and C, reactions mainly confined to crows and gulls are treated. In Section A, however, a certain behaviour called circular escape flight is mentioned. That behaviour is typical of DUCKS of any kind and of *Anser fabalis*. (Although some observations of the behaviour in question were made also in other *Anser* species, the material obtained does not hold any assurance that the reactions have not been induced by the more numerous *A. fabalis*.) Circular flight of ducks seems to be a common response to eagles hunting on a lake. The following species have caused this reaction: *Aquila chrysaëtos*, *A. clanga*, *A. pomarina* or *clanga*, *Haliaeetus albicilla* and more seldom *Accipiter gentilis*, *Milvus milvus*, and *Pandion haliaëtus*. The ducks involved in the behaviour have been, as a rule, *Anas* sp., namely *A. platyrhynchos*, *A. crecca*, *A. penelope*, *A. clypeata* and, besides *Mergus merganser* and *M. albellus*, sometimes also *Aythya* and *Bucephala*. As mentioned above, *Anser fabalis* has reacted in this way to hunting golden eagles in some instances. The behaviour is also noted in *Gavia* and *Podiceps*, especially in *Gavia stellata* (MARKGREN 1959). Occasionally the behaviour was noted in other species of ducks than those mentioned. Probably the actual behaviour is a response to more than one impulse, as, for instance, (1) the impulse to *escape*, (2) to *alight* on the water, and (3) to keep the predator in sight. (For similar complicated reactions, cf. SVÄRDSON 1949 C, TINBERGEN 1951.)

This suggestion is based on observed details of the behaviour of ducks in "circular flight". It has thus been seen how the birds have returned again and again to the place they have risen from, as if to alight, but then have risen again with
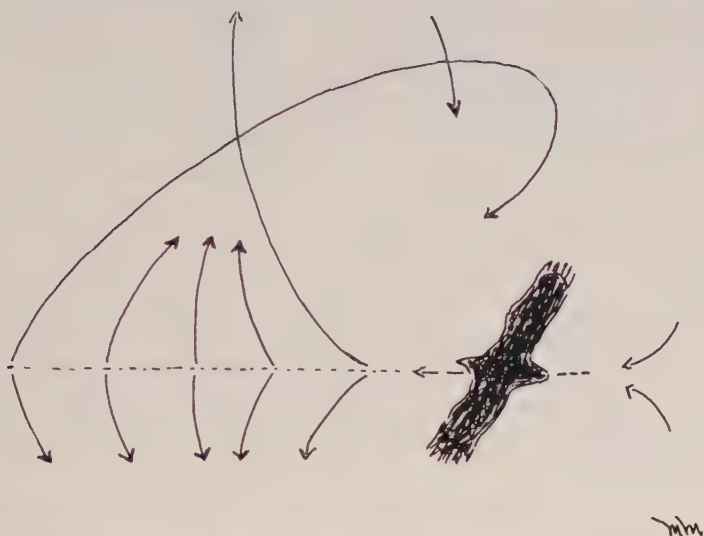
The motion curves of herring gulls eluding the danger (an eagle) by circuitous or elliptical flight.

alarm, sometimes having touched the water. The birds have not seldom gone on with their circulating long after the disappearance of the bird of prey. It was also observed how the ducks followed the predator in an extended curve, just to keep the danger in sight. This typical circular flying will be seen over lakes but it will also occur in a more elliptical form along brooks, when ducks are flushed from their waters.

E. *Eluding the Danger by a Circuitous or Elliptical Motion Curve*

All the patterns mentioned are interesting indeed, not so much because of the form of the curves performed by the birds but because of the probability that these reactions are the adequate response to the actual disturbances. It is probable because the same peculiar behaviour is seen to occur repeatedly in a quite enormous number of birds in similar situations. It is the most outstanding behaviour, however, that will be treated in this last part of the chapter. It must be said at once that this behaviour is found in *Anser fabalis*, in *Anas platyrhynchos*, *A. crecca*, *A. penelope*, in *Aythya* and less pronouncedly in *Mergus* but is principally seen in *Larus* and especially in *L. argentatus*.

The behaviour is best studied on a cold, early winter morning at Sjölunda with a slight off-shore wind. The gulls will then be found quite close to land, almost apathetic with cold, their critical distances being reduced to a low value. The birds' incentive to sleep is then great, and many birds actually do sleep. All the common gulls, many black-headed and also some herring gull or other will be found asleep. Only *Larus marinus* is likely to be fairly unaffected by the adverse weather. If a *Falco peregrinus* or a *Haliaeetus* at such a moment appears on the

hunt low over the ice, then the fugitive reaction of the great flocks of gulls is very likely to be the *elliptic eluding curve*. The taking-wing reaction will propagate as a wave in front of the predator, whereas the birds just passed and out of danger are likely to be returning to their original places. In front of the falcon (or eagle) and proximally, the gulls are in flight at both sides of the flying direction of the predator, at first outward and away from the falcon, then returning inward as the bird of prey goes by. The curve line is thus forming an ellipse with the longest axis making an acute angle with the flying direction of the predator, the angle pointing backwards, whereas the corresponding angle is obtuse as regards the motion curve of the distal flocks, i.e., the initial escape curve close to the danger zone will be directed onward away from the predator, whereas the evading movements distally but in front of the bird of prey will be circuitous and directed obliquely backwards, both curve motions ending with the return to the earlier position of the birds.

This behaviour in its simplicity may be an almost perfect response to the disturbance of a hunting bird of prey, allowing the gulls to escape the danger, watch the predator and, last but not least, to return to their places, all with perhaps some few wing beats. When the hunt and the gulls' fugitive reactions are observed from the side and at a moderate distance, it looks as if the distal flocks of gulls are flying towards the predator. But it is also seen that the hunted birds are describing a vertical curve, i.e., the motion plane is at an oblique angle with the horizontal plane.

Hunt and escape will thus form a pattern, the structure of which is much dependent on outer ecological elements and above all on the birds involved. If a hunting predator changes its direction of motion repeatedly, or if it changes its manner of hunting all of a sudden, or if it does something strange, then the behaviour pattern of the hunted bird is likely to be chaotic to the observer. Predators not seldom make a choice of bird to be hunted that is scarcely to be understood.

THE ASPECT OF INTERACTION BETWEEN PREDATOR AND PREY IN HUNTING AND ESCAPE

1. Introduction

In the discussion above the aspect of interaction has occasionally been mentioned especially in Chapter III. Here in Chapter IV the problems concerning that aspect have to be treated in more detail. Although hunting and fugitive behaviour are possible as independent phenomena accidentally, they are actually explicable only as mutual interaction. The subject is wide and complex and presents many intricate problems. For that reason the matter will be restricted. Another reason for this restriction is that we can expect discussions on the subject by G. MARK-GREN, who is doing ethological and ecological studies of geese and eagles in Scania. Important work on the interaction of predator and prey has been done from the ecological point of view. Most worthy of mention are the works of ERRINGTON (1946, 1956), who has inspired many Scandinavian ecologists. K. CURRY-LINDAHL has thus elaborated an important series on Swedish mammal and avian predators. Here his work (1950) on *Bubo bubo* will be mentioned (cf. BODENHEIMER 1938, SVÄRDSON 1949 A).

In this connection the *interaction* will be treated only from an *ethological* point of view. Now and then our subject has been touched on, mostly in short notes, in the ornithological periodicals of the last twenty years. Also the modern handbooks on birds contain some observations on the mutual behaviour of predators and prey (NIETHAMMER 1938, WITHERBY 1945, LØVENSKJOLD 1946, SALOMONSEN 1949, SVÄRDSON & DURANGO 1950, CURRY-LINDAHL 1959 B). In this connection the paper on the sparrow hawk (*Accipiter nisus*) by TINBERGEN (1946) should be mentioned. RUDEBECK (1950 B, 1951), discussing the modes of hunting of predatory birds, has also given information about the behaviour of prey birds and of the interaction; to this important paper we will return in further discussion. In this part of the present paper the discussion will be confined to the *simultaneous interaction*.

2. Hunting Behaviour and Predacious Activity

A. *Introductory Discussion*

The hunting concept may be used in many different senses. RUDEBECK (1950 B) writes on the sparrow hawks: "They are often observed to fly very low, on a combined hunting and migration flight. They approach with moderate speed, glide smoothly in among the bushes and dense saplings; they even follow the contours

of every knoll and have an incredible ability to hide behind the smallest irregularity. They are always prepared to attack." (RUDEBECK 1947; the original is in Swedish.) Here we have *hunting* (*flight*) in the sense of flying *prepared to attack*, a behaviour that does not exclude *migration flight*. This behaviour may be synonymous with being *"on the look-out for quarry"* (RUDEBECK 1950 B).

RUDEBECK (1950 B) has, however, defined as hunting "those cases which should really be called hunting, viz., when a bird of prey makes one or more completed attempts to kill or seize a specially selected quarry". These cases should be distinguished from "incompleted attempts at hunting". With the quoted definition of the concept we find that (1) hunting is confined to *predatory birds*, (2) the attempt to *kill or seize* has to be *completed*, i.e. the interrelation of the motion curves of the birds involved has to be favourable for seizing, (3) the hunting is confined to the behaviour *after the predator has selected* a single bird out of a flock.

Hunting in the sense of the definition above is, however, also found outside the birds of prey. The herring gulls of arctic Norway are seen to seize, kill and engulf sick or young kittiwakes or ducks, sometimes even seizing the quarry in the air. *Larus argentatus* is also found occasionally to hunt passerine birds (ANDERSSON 1957). Rarely the crow (*Corvus corone cornix*) is also mentioned as hunting and killing small birds (MATTSSON 1948).

The selection of a single bird out of a flock may be regarded as an action that limits the "hunting" from other behaviour. In many cases that definition will make it easy for the observer, as much of the predatory activity concerning the prey would then be put down as "attempts". On the other hand, the very delicate indications of interaction are likely to necessitate regarding the behaviour of the bird of prey as a unit, when the activity of the predator is controlled by the *raptorial motivation*.

A completed attempt of the predator to kill or seize a quarry may as a phenomenon be easily distinguished from an "incompleted attempt at hunting" in a case where the motion curves of the birds intersect, but less obvious in conlinear movement. Another complication is found in the probable behaviour of a predatory bird whose *raptorial motivation* is strong. In such a case the bird of prey is likely to be too sensitive of the presumptive quarries, i.e. to be inclined to react raptorially also, when the temporal-spatial relations of predator and prey do not favour the former.

Actually, what RUDEBECK (1950 B) has defined as "hunting" could very well be called "attacking". "Incompleted attempts at hunting" would then be changed to "incompleted attacks" or in some cases "incompleted chasing" or "persecution". Some arbitrary definitions of predatory activity are drawn up below.

B. *Definitions*

1. *Predacious activity.* The *foraging activity* of raptorial animals (even the sedentary predators). The behaviour of occasionally raptorial animals and the arduous searching for a quarry or a *carrion* in many birds of prey is also included.

2. *Hunting*. The predacious (or raptorial) activity of an animal on the *move*. RUDEBECK (1950 B) writes: "Frequently a bird of prey is seen in flight, searching for quarry or at least prepared to attack if any quarry should appear".

3. *Chasing*. The hunting is *directed* to a certain perceptible group of animals or to a selected prey. Synonym: persecuting (among others).

4. *Attacking*. Chasing at the instant of an attempt to seize or kill one selected quarry, or chasing at the temporal instant of converging motion curves of predator and a group of animals (birds). The attack may take place as a pounce, a *swooping*, an *accelerated persecution* and so on.

Raptorial activity during migration is a very common phenomenon in predatory birds. RUDEBECK (1950 B) has pointed out that "Birds of prey very often turn from migration flight to hunting if a suitable opportunity presents itself. This is particularly true of the sparrow-hawk, merlin and peregrine falcon, but can also be said of sea-eagles, marsh harriers, and others." This statement is important; it is made without exemplifying data, not because of any lack of instances, but rather because of an enormous multitude of examples. The present author could also have listed numerous instances of such behaviour. Some data are given in the tables, however. To the typical species named by RUDEBECK the present author would add *Pandion haliaëtus* as a frequent hunter on migration along the sea coast, and *Falco tinnunculus*. As regards the raptorial birds that prey on other birds, the "hunting on migration" is seen to be initiated by the appearance of the prey at a short distance or in an accessible position. RUDEBECK (1950 B) suggests that "it may be assumed that the bird of prey attacks when the quarry has a certain position in relation to the bird of prey. Perhaps one can also assume that the attack is released most surely and automatically, i.e., that the "desire to attack is strongest", at the moment when the quarry is in such a position that the chances of successful hunting are maximal." He thus suggests an *interaction* at the initial moment of hunting in the sense of *chasing* (see above). Whether these predators are to be regarded as primarily migrating or hunting should be decided by continuous observations in each single case. But, apart from that, the interaction between predator and prey at the initial moments of chasing is obvious. The interaction is also shown by the initiation of fugitive behaviour in response to the appearance of a bird of prey. Now, in order to trace the mutual relations, we return to the activity of the predatory birds.

3. Predacious Activity and Non-raptorial Behaviour of Birds of Prey Causing Escape

A. *The Reactions to Non-raptorial Activity*

Even on close observation it may be difficult to decide what is predacious behaviour and what is not. Thus, a raptorial bird watching the presumptive prey from an observation place or a predator on actual migration may be in a state of strong raptorial motivation. But it may be that the *resting* or *migrating* urge

is also strong. In that case the behaviour of the prey is likely to be decisive for further action. The threshold of response to the prey will in any case be dependent on external stimuli and internal motivation (TINBERGEN 1948). Without the appearance of a presumptive quarry nearby, the raptorial activity would perhaps have been "hidden" from observation. Anyhow, the behaviour of a migrating predator that does not react in an observable way to the appearance of prey but just goes on with migration will be put down as *migratory behaviour*, regardless of the (not observable) raptorial motivation.

B. *Reactions to Steady Migration Flight and Soaring*

This migratory behaviour is defined above, where it has been suggested that it is a reaction to slight thermal air currents. At a locality such as Falsterbo, it may also depend on impulses to rise over the sea. The single predators or sometimes a veritable flow of birds of prey, will be seen to go out rising over the sea, although some of them may have lost height already over the nearby little island of Måkläppen (cf. RUDEBECK 1950 A, p. 84, Plate 1), where *Larus* sp. and ducks are usually resting. Over Sjölunda, also, the birds of prey on spring migration are likely to present a downward curved steady migration. The behaviour of soaring predators is quite similar at both localities.

Surprisingly, it is found that the herring gulls of Falsterbo are not seen (by the author) to react fugitively to *Buteo, Pernis, Circus, Milvus* or *Falco* on steady migration or on soaring over the sea, whereas the same behaviour will mostly cause taking wing in the *Larus argentatus* of Sjölunda. Maybe the height of the migrating predator, the direction of the motion curves and probably some differences in the frequency of raptorial birds over the localities plays a part. The difference, however, is a fact. It may depend on either the behaviour of the migrating predators or the sensitivity of the gulls. The migratory birds of prey in spring reaching the Scanian shore near Malmö have completed a migration over the sea. Their internal raptorial motivation is likely to be increased, whereas the urge of migration ought to be decreasing at that instant. As a matter of fact, hunting is a common behaviour of the raptorial vernal migrants of Sjölunda. It may be that there is something "predacious" in the behaviour of these birds of prey, something that the gulls are sensitive to, although it is not understood by the human observer. On the other hand, as the gulls — and other birds of Sjölunda — have been hunted during the early spring and actually are often hunted by predatory birds on vernal migration, they are likely to react sensitively to any raptorial bird, even soaring or on steady migration. Steadily migrating eagles (and *Pandion*) passing low over Måkläppen are seen to cause escape reaction.

C. *Reaction to other Slow Movements of Predatory Birds (Gliding and Hovering)*

Soaring has been treated above as part of migratory activity (cf. RUDEBECK 1950 A). Also *gliding* is often seen alternating with soaring in migrating birds of

prey (*Buteo, Pernis, Aquila, Haliaeetus* and somewhat modified in *Pandion* and *Milvus*). In the case of a bird (soaring and) gliding at a considerable height, 100–400 m or more, no escape reactions are found in the gulls of Falsterbo and Må-kläppen, whereas fugitive reactions are typical of the vernal population of gulls at Sjölunda. (The differences in behaviour are discussed above; see (a).) *Gliding low* is a behaviour which usually causes fugitive reaction in gulls and ducks of the Scanian localities. This behaviour is especially noted in eagles and also in *Pandion, Circus* and *Milvus*. When these birds of prey are gliding low over the ground, small passerine birds, such as *Alauda, Emberiza citrinella, Anthus, Fringilla* and *Carduelis*, will also react by *taking wing*, thus demonstrating that the critical distance is very little in these birds. It is most interesting, however, that they react on the appearance of great birds of prey in gliding flight. At Sjölunda, gliding is not seldom noted in owls (*Asio*) with a taking-wing reaction of short duration as a result in the herring gulls.

The *hovering* of *Pandion, Buteo*, and many species of *Falco* is not seen to awake escape reactions, except in small passerine birds on the ground below the predator (*Alauda, Anthus. Emberiza, Carduelis*). The reactions to the slow motion of predatory birds thus vary somewhat in different cases. We now turn to the question that has to be answered in this connection, viz. what part does recognition of raptorial species play in the escape reactions observed? a subject that has now and then been touched on above.

4. Observable Recognition of Raptorial Birds

It is a commonplace suggestion that most bird species not only should be able to "recognize" raptorial birds but also to distinguish the different species of predators and thus to adapt their reactions according to degree of danger. However, this suggestion seems questionable, as many birds do not behave in that way. The avian recognition of predators is a fact, although the recognition is not perfect (HEINROTH & HEINROTH 1928, TINBERGEN 1936, 1951, 1953, 1958, RUDEBECK 1950B, 1951, HARTLEY 1950). Very often non-predators are "recognized" as raptorial birds, or rather they provoke escape reactions just as the birds of prey and the simple predatory dummy models do. In order to facilitate our discussion of what the prey is reacting to, we will make a schematic classification of the raptorial birds into types. The classifications used above as regards the mode of movement of the predators will be used here too.

A. *Characterizing the Predators and the Reactions to Them*

TYPE I. *The gyr-falcon type*

Falco rusticolus, F. peregrinus and *Accipiter gentilis* are classified as belonging to this type.

It must be mentioned immediately that these predatory species, although they

have much in common, are yet different in appearance, behaviour and general habits. The powerful lashing flight of *Falco peregrinus*, the waving or rowing or even winding wing-beats of the gyr falcon and the powerful, but nevertheless flapping flight of *Accipiter gentilis* will not be confused by any careful observer. Their inter-specific differences will also be quite visible in their typical methods of hunting, viz., a goshawk hunting by surprise attack like a sparrow-hawk, a peregrine killing its prey by a swoop and a gyr-falcon in steady undulating flight, hunting low over the ground at considerable speed for miles. Nevertheless, the predators in question have much hunting behaviour in common. They are all seen to hunt by *pouncing, swooping, rectilinear acceleration* and *low steady hunting* some metres above the ground. Like most birds of prey, they are excellent at soaring, often to a considerable height. In such cases they look very similar to the human observer.

The recognition of these three species as predators is almost perfect in *Larus argentatus*, *L. ridibundus*, *L. canus* and in the *Anas* species of Sjölunda, as well as in the crows. Type I is recognized at that locality, regardless of the actual behaviour of the raptorial bird in question. And the reaction is just the same in all cases, viz. most gulls, crows and ducks take wing. Observed failure of the gulls' escape reaction to a nearby flying *Falco peregrinus* was noted only *once* at Sjölunda by the author on a very cold and foggy winter morning, when the gulls were, as mentioned, almost apathetic. It should be mentioned that *F. peregrinus* and *F. rusticolus* do not always capture prey in the air, but also pick up mammals or birds from the ground. On their food, see JOURDAIN in WITHERBY *et al.* (1952). Only seldom is *F. peregrinus* seen to cause escape in *Anser*.

If Type I is characterized by predators powerful in outline and movements and by a certain moment of inertia expressed in accelerated swooping or gliding, the next type comprises the small falcons.

TYPE II. *The merlin type or small falcon type*

Falco subbuteo, *F. columbarius*, *F. tinnunculus* and *Accipiter nisus* are included here, as also *Falco vespertinus* and *F. naumanni*.

Mutatis mutandis these predators may be said to hunt and behave like the bigger birds of Type I but lack the power, gravity and enormous acceleration of their larger relatives. Also these birds hover better and more frequently than the birds of Type I.

None of them is ever seen to hunt a *Larus argentatus*, but the merlin, the kestrel and the sparrow-hawk often hunt passerine birds (and sometimes waders) at Sjölunda. The above-mentioned predators also migrate over the locality, especially in spring.

To predators of Type II on vernal migration in steady flight with some soaring and gliding with the wind, the gulls and many other birds often react fugitively by *taking wing*, (see the Tables on the species). As a matter of fact, there will always occur some fugitive reaction in any of the birds of the locality in such cases. To the *swooping* of wintering merlin, escape reaction is also noted in the herring

gull, *Corvus* and *Anas*. But no escape reaction is caused in these birds by hunting kestrel or sparrow-hawks in winter.

The two following types are less well defined than I and II.

TYPE III. *The harrier type*

Species belonging to the genera *Circus* and *Milvus* are representatives of this group. What they have in common is, above all, slow gliding and soaring on slight upwinds and a rather slow flight with somewhat easy or lazy beats of the wing and in addition hunting by way of exploring the fields in a slow flight close to the ground. They also hover at times.

At Sjölunda the predators of Type III have provoked the *taking-wing reaction* in *Larus*, *Corvus*, *Anas* and some other groups of birds, when these predatory birds have been on migration and hunting (see the Tables).

Perhaps the birds of prey in question by chance pick up sick birds. The author has never noted such a case, but some peculiar behaviour points in that direction (cf. *Buteo* below). These birds are indeed rather slow, as is also the following group.

TYPE IV. T*he buzzard type*

First we find *Buteo buteo*, *B. legopus* and *Pernis apivorus* in this group (to some extent *Pandion* also has to be included here). During the winter there are always buzzards *Buteo buteo* and *B. lagopus*) in the Sjölunda area. These buzzards are often seen to hunt (and actually kill) sick ducks. They also take some interest in almost dead gulls, and they can be seen trying to capture some small bird in the fields. In their hunting and on gliding out over the gulls they often cause escape reaction. During vernal and autumnal migration these predators also induce the taking-wing reaction. All of them (*Buteo*, *Pernis* and *Pandion*) are seen on migration, both in *steady migration* flight and in alternating *soaring* and *gliding*. Usually the gulls, often also crows and ducks, take wing. However, although these birds are soon found to "ignore" an osprey fishing, hovering and stooping, nevertheless they are likely to show escape reaction to the same predator going out over the sea after a long rest in the usual slow flight with gliding intervals. The osprey has to be included in the next group of predators, too, as it is in many ways intermediate.

TYPE V. *The eagle type*

Here we find *Aquila chrysaëtos*, *A. clanga*, *Haliaeetus albicilla* (and *Pandion*). The usual occurrence of the osprey is mentioned above. Here, as regards the presence of eagles on the Scanian coast, it must be said that they are oftener observed by the author hunting than on migration. Migrating eagles at a very great height may have been overlooked, however. In their hunting the eagles appear in flight with powerful wing-beats alternating with gliding, as a rule not more than some twenty feet above the ground or the ice. Usually they are observed in time by the gulls, crows and ducks, which take wing and behave as described

above, the diving ducks just swimming slowly away from the course of the predator with only some intention movements of diving or taking wing. Except for these great flocks of diving ducks, the presumptive prey is likely to be out of reach of the predator. But as the eagles are often seen to explore a vast area while hunting and are not seldom likely to return in the same way repeatedly, the hunt will not always be in vain. Some duck may be left behind when others rise or it may try to dive. In such instances, the hunt will continue with the attack. *Haliaeetus* and *Aquila clanga* are seen to charge birds in the air, on the ground and on the water with success (see the Tables; cf. also MARKGREN 1951, 1959). Hitherto the author has not observed *A. chrysaëtos* attacking birds on open sea or in lakes. On the other hand, ducks in brooks or just at the shore are attacked (cf. G. MARKGREN 1960). In the actual attack, performed as a linear acceleration or as a sort of swooping or pounce, the eagles show a swiftness and a rapidity of motion of quite another order than their well-known slow hunting behaviour by way of looking out for a quarry or carrion. Nevertheless, the powerful swooping or the moments of speedy chase are typical behaviour of the species discussed, although their slow gliding or steady flight with heavy wing-beats may be better known to man and is obviously also "recognized" by the presumptive prey. The survival effect of fugitive reaction to the eagles in their slow or even "lazy" hunting behaviour depends on a decreased probability of predation upon the reacting birds and, on the other hand, a decreased probability of successful escape of the birds that ignore the slow eagle and react fugitively only to the violent attack.

The diving reaction to eagles in diving ducks is sometimes dangerous, especially when two or more eagles are hunting simultaneously. Diving ducks are thus seen to be captured on water by eagles (see the Tables).

5. Fugitive Error Reactions, Errors of Interspecific Identification in Birds, the "Arm Test"

TINBERGEN (1936) has pointed out that errors in avian interspecific recognition are most frequent in reactions to raptorial birds "for which swifts and pigeons are often mistaken by birds". HARTLEY (1950) suggests "that the complex of visual characters by which a fast-moving predator is recognized will be simpler than the configuration of characters for a more slowly moving or stationary enemy". Escape reactions in error are indeed very frequent in gulls, ducks and in the genus *Corvus*. Herring gulls may be seen to take wing for a little male merlin on swooping or even for a swift or a falling piece of wood. It may be, however, that escape reactions to slowly moving birds are more common, where eagles hunt frequently. It is thus probable that the sensitiveness to hunting eagles has much bearing on the (erroneous) escape reactions noted especially at Sjölunda in *Corvus corone cornix*, *C. monedula*, *Larus argentatus*, *L. ridibundus* and *Anas* to a group of species that are mostly quite harmless to the birds mentioned.

A. *The "Eagle-like" Predatory and Non-predatory Birds*

Ardea cinerea, Botaurus stellaris, Ciconia ciconia, Buteo buteo, B. lagopus, (Accipiter nisus), Milvus milvus, Pernis apivorus, Circus aeruginosus, C. cyaneus, C. pygargus, Pandion haliaëtus, Grus grus, Asio flammeus.

(a) *The sparrow-hawk (Type I, II or V?)*

In the above list the recently discussed predator types (II) III, IV and V are represented. But the little sparrow-hawk is put in brackets, because of its special behaviour on vernal migration (at Sjölunda). It has already been mentioned that *Accipiter nisus* is one of the predators which are often seen in combined migration and hunting, as is pointed out by RUDEBECK (1950B). In those instances, when the migrating sparrow-hawks have acted as disturbances, events have usually taken the following course: (1) a taking wing in gulls, ducks (and waders) is observed; (2) by the propagation of the reaction wave in the bird flocks the probable position and moving direction of the hawk is found; (3) this is actually found after looking in the probable direction; (4) now the sparrow-hawk is often seen to be either actually hunting or at least approaching in a downward curve or it may be found soaring and gliding at a considerable height. It is thus difficult to say if *A. nidus* is primarily causing escape reactions as a living *"eagle model"* or as a fast-moving hunter of Type I–II. The reaction to some of the other birds will be discussed.

(b) *The heron, the crane, the stork and the bittern*

The members of this group of slow-moving birds with powerful though heavy flight are somewhat eagle-like in their movements. In *Ardea cinerea* the curved neck will make the bird still more similar to an eagle. But escape reaction in *Larus, Anas* (and *Corvus*) to *Ardea* has also been noted when the heron has been flying with extended neck after taking wing. It is suggested that the escape reactions to the heron in that case and to the crane, stork and bittern are reactions to *outline and movement of wing.*

B. *The Dummies or Models and the "Arm Test"*

(a) *The dummies*

The famous experiments with models of predatory birds have shown that the avian fugitive reactions to birds of prey are not only responses to the entirety of the predator but also, at least to some extent, to single qualities of the raptorial birds. These characters are signals or releasers of escape behaviour. For discussion of the problem, see TINBERGEN (1951). From these experiments it is known that the outline of neck in relation to wing (*short neck*) and the movement of the whole bird have a bearing on the escape reaction. The results of the "arm tests" made by the present author suggest that wing movements are also signals or releasers of

fugitive reactions. Here we note, too, that the herring gulls of Sjölunda are seen to react fugitively to the buffeting of scavengers but not to other movements of man in category II (Chapter IV above), not even to throwing movements. The buffeting scavenger is thus making a sort of "arm test", i.e. he is acting as a model of a flying predatory bird.

(b) The "arm test"

In the "arm test", as well as in the flying movements in disturbances by birds of the "heron–stork type", there is a quality of heavy motion of long wings that is also typical of the "eagle type" of predatory birds.

A modified "arm test" experiment series with pieces of apparatus is planned by G. MARKGREN and the author. As mentioned before, the "arm test" is called in the notes "eagle test" (örnprov) just because of the distribution of positive reaction to that species. It is obvious that the same species that react to eagles by taking wing react in the same way to the "arm test" and that those who do not react positively to eagles, if not very close, are not sensitive to the "arm test".

C. The "Recognition" Concept

As is seen above, the interspecific as well as the intraspecific recognition is at the same time both very poor and in a way outstanding (cf. TINBERGEN 1951, 1953, LACK 1953). The reason for the seeming contradiction is largely that "recognition" may mean different things, as will be seen below.

(a) Individual recognition or recognition of single individuals like mate or offspring

This recognition has to be perfect or it is of no value to the bird and the species. TINBERGEN (1953) points out that there are observations that seem to show that both partners find and recognize each other in spring by their return to the colony. He has observed that the voice plays a part in recognition, as well as visual stimuli. A herring gull may "recognize its mate in flight at 30 yards distance" (TINBERGEN 1953). According to LORENZ (1931), the jackdaws (*Corvus monedula*) of a colony are able instantly to recognize the members of their colony, in which there is a rigid hierarchical order (a sort of "pec order"). The recognition of a sexual partner is not necessarily intraspecific. Thus in 1950 the author observed at Sjölunda a *Casarca ferruginea* that was obviously recognizing a female *Tadorna tadorna* as its mate (cf. that the "Prägung" of a bird may be directed to a human person, for instance, according to LORENZ 1952; cf. FABRICIUS 1951). From available facts it is "evident that the Herring Gulls are monogamous" (TINBERGEN 1953). (It could perhaps give some information on the mechanism of partner choice to find out by observation if the (intraspecific) individual recognition in polygamous birds is poorer than that in the monogamous species.)

The personal or individual recognition is, however, a phenomenon beyond doubt, but many observations will have to be made to allow of a comprehensive discussion of the subject. As already mentioned, the voice seems to play a part in

recognition (BRÜCKNER 1933, TINBERGEN 1953). According to HEINROTH (1911), the facial expression is also probably of importance for the recognition mechanism (cf. the rôle of the face of the owl in predator recognition, HARTLEY 1950).

(b) *Recognition of strangers*

According to TINBERGEN (1953), there is an amazing ability instantly to recognize strangers in a colony. "When we saw this for the first time, we thought that recognition of a stranger might be due to its uncertain behaviour, for as a rule a bird, while behaving in a rather self-possessed way on his own territory, is ill-at-ease when on strange territory. However, this is not always the case. Especially when a pair is temporarily absent, or when one bird is incubating, which ties him to the nest, strangers may trespass and make themselves quite at ease, behaving "as if they were at home". Yet as soon as the owner(s) return or an incubating bird is relieved, the strangers will be chased." (TINBERGEN *op. cit.*)

This is most interesting and has a great bearing on the psychical powers of birds. The ability to recognize a stranger is probably partly founded on behaviour typical of a bird intruding on a territory. In the discussion of predator recognition a certain "strangeness" theory has been proposed (NICHOLSON 1927) and has been tested in different ways by HARTLEY (1950) in his paper on interspecific recognition. The results were not positive. Returning to the intruding stranger, however, we find that he is not attacked and chased indiscriminately. The attack is mainly released in the territory holder by reproductive activity on the part of the stranger (TINBERGEN 1953). If the trespasser is inciting attack by some behaviour or other, he is not necessarily identified or recognized as a stranger. But if he is releasing hostility merely by his existence in the territory without any provoking attitude, that relationship could possibly mean the existence of an avian power of identifying *a lack* of familiar qualities. That would indeed mean a mental power beyond the reaction to single releasing signals.

(c) *Recognition of predators*

In identifying predators, the typical characteristics of a whole group of beings, not merely the "face of a single person" has to be recognized. Indeed, a working mechanism of enemy recognition has to be sensitive to anything that has a slight similarity to a dangerous animal. There is for the bird usually no chance of studying individual enemies to learn their facial expression. On the contrary, the personal relationship may be fatal to the bird. In other words, the surviving birds are those which react "in error", even to slight indications of a predator, rather than those which respond only to most pronounced traits. The discussion of the surviving effect of reactions to predators would be to some extent a discussion of the evolution of interspecific (and intraspecific) predation and escaping. But it would be beyond the scope of the present paper to touch on that subject. However, regardless of whether the frequency of predation on birds has decreased or increased or has been on the average at a constant value in the present species, the

surviving mode of behaviour has to be balanced between extreme values of reaction sensitivity to predators or what is similar to the predators. It means that a certain part of the surviving birds have to be reacting "too" sensitively. A great part will thus react primarily to predators and non-predators with qualities similar to the characteristics of predators; and a considerable part of the other birds are likely to be caught in secondary reaction by induction (TINBERGEN 1951, ALTMANN 1956). The induction effect is easily observable in migratory behaviour (DAHL 1936, OTTERLIND 1944, 1954, MALMBERG 1950, MARKGREN 1951 B, 1957). In the disturbances by predators and the escape reactions there will be a certain interaction also on a great scale. The more specialized the predation upon a bird species, the more exclusive is the reaction in the species allowed to be. And the more general (and frequent) the predation on the species, the more it will be found to show escape reactions to "harmless" phenomena, i.e. to non-specific disturbances. That is to say, the releasing signals are many in these birds. A brief discussion of some of these releasers follows.

(d) *Some escape-arousing properties of predatory birds*

As has often been mentioned, fugitive behaviour is released secondarily by induction from the members of a group, a colony or even by birds of other, more or less related (or familiar) species. These releasers are the *alarm call*, the fugitive *intention movements*, the *mobbing reactions* or other display behaviour and the *taking wing*. Most of these releasing reactions show great interspecific variation and have to be treated by species, which cannot be done here.

We will now turn to the releasing signals that are elements of the predator recognition in the reacting bird.

SHAPE (OUTLINE AND CONTOUR)

1. *The short neck* in *Strigiformes* and *Falconiformes* (TINBERGEN 1948, 1951, HARTLEY 1950). That quality, however, is not found only in raptorial birds. Probably also the "escape in error" from flying heron is partly dependent on this character (see the discussion of predator types above). The model experiments by TINBERGEN and others (1951, 1953), as well as the flying predators, represent a disturbance not merely by outline but in their outline on some part of their motion, usually a headlong forward motion (see below and HARTLEY 1950). The combination of short neck and flight with whirring beats of small narrow wings in puffin and little auk (*Fratercula* and *Alle*) does not seem to mean an escape releaser in other birds.

2. *Solidity in contours of body* (or the Impression of Solidity, HARTLEY 1950). That quality is an "*Owl-Valence*" (HARTLEY *op. cit.*) found by experiments.

3. *The pointed wing.* This is a quality of the falcon wing and may play a part in the combination of releasing signals of a group of predatory birds (Chap. XL, types I and II, as regards *Accipiter nisis* only in certain moments of motion). The often-observed "escape in error" from *Apus apus* (HEINROTH 1928) and pigeon (TIN-

BERGEN 1951) may to some degree be due to a wing character. This wing character may be of significance in some, and not so few cases, when taking wing in escape has been observed by the author in passerine birds as a reaction to flying birds of the following species: *Columba palumbus*, *C. oenas*, *C. livia*, *Apus apus*, *Charadrius apricarius*, *C. morinellus*, *Numenius phaeopus*, *N. arquata* (seldom). Of interest here are six observations of escape reaction in starlings (*Sturnus vulgaris*) to *Cuculus canorus*, four observations when the reaction to the cuckoo has been entirely escape—not mobbing — in *Motacilla* and *Anthus* in spring and about ten observations of taking-wing reaction to the cuckoo in small passerine birds (probably *Anthus* and *Carduelis*) in August and September.

The effect of "sudden appearance" probably has played a part in some of the above-mentioned cases but not in all of them. As is easily seen, only a few of the birds mentioned above are characterized by a short neck.

4. *The angular wing.* In the famous experiments by LORENZ and TINBERGEN the "shape and size of wings and tail, were rather irrelevant" (TINBERGEN 1951). The shape and size of the *wings*, however, is probably not entirely irrelevant to the reactions to raptorial birds and it may play a part in certain experiments too. In some cases *Larus argentatus*, other species of *Larus*, *Anas platyrhynchos*, and a few other species have reacted with escape to aeroplanes with a very long "neck" (long but thick). There are also to be taken into account all the escape reactions to "eagle-like" non-predators (Section 5 A) (*Ardea* with extended neck, *Ciconia*, *Botaurus* and *Grus*), where these birds are not known by the local bird population. The angular wing is that of the predators type V and IV (Section 4).

It is suggested above that in our discussion of escape releasers or signals we have to take into account both shape of neck and shape of wings. But motion may also be a stimulus in the visual domain. TINBERGEN (1951) also mentions "sudden appearance" and "type of movement" (cf. also HARTLEY 1950).

The type of movement will be treated below. The motion of the whole bird is briefly discussed. It will also be treated from a special aspect. First, however, we consider the wing motion (cf. also the discussion in 3. below).

WING MOTION

1. *Characteristics of wing motion.* The wing of a bird in steady flight may be said to describe complicated motion curves composed of vertical swinging about a horizontal axis (the long axis of the body) and simultaneous horizontal swingings of arm and hand in the extended body plane, these movements combined with certain periodic torsional movements. The whole motion pattern is thus to be described in three dimensional curves. But to an avian observer (or a man) looking at a flying bird from behind or in front, the motion pattern may be simplified into a periodical change in length and outline of wing and to the vertical swinging, of which we also think when describing wing motion with expressions such as "fast, easy, lazy, slow, heavy" and so on. Indeed, this point of view is essential to wing motion, as it is often just what the human or avian observer

will realize. Thus, simplifying the wing motion and neglecting some special patterns in small passerine birds, we might describe some of the avian wing movements by the following characteristics. (1) *Amplitude*. The wing beats may thus be said to be both high and deep, as in *Asio flammeus*, or only high, as in *Aquila chrysaëtos*, or only deep as in *Ardea* and *Botaurus stellaris*. (2) *Frequency* of wing beats, that is, high-frequency or rapid wing beats, as in *Accipiter* (*nisus*), or *moderate*, as in *Buteo* and *Circus*, or of low frequency, a flight with slow wing beats, as in *Ciconia*, *Grus* and *Haliaeetus*. (3) *Finish of the active downward movement*. We talk of a lashing wing beat, an accelerated finish, as in *Falco peregrinus*, or an even wing beat, as in the steady flight of *Buteo buteo*, or a lazy wing beat as in *Milvus milvus*. If we want an analysis of flight from an aerodynamic point of view, the problem is quite different. Here it is merely a description of easily observable qualities in the wing motion. Some characteristics of flight are distinguished according to the motion of the whole bird, not merely the wing. Here should be mentioned the quality of "heavy" or "easy" flight. *Haliaeetus* is heavy of motion, even without moving the wing, just in soaring and gliding. It may be that the presumptive prey is enabled to realize that quality.

RUDEBECK (1951 B) has mentioned some cases of the "swallow flight" or "thrush flight" of the merlin and has briefly discussed it. GEYR VON SCHWEPPENBURG (1942) also has observed that particular hunting behaviour. It is of special interest that on these occasions the hunted swallows showed no fear. Also in some of the cases related by RUDEBECK the merlin was flying in the close vicinity of a whole flock of small birds without causing escape reactions. On other occasions the bird flocks reacted fugitively to the predator. Among the instances noted by the present author, too, there are a few cases when the falcon has not caused fear in the birds attacked.

Summarising, we find (1) that small passerine birds in some cases do not show escape reactions to a typical predatory bird, the merlin. We suggest that the reason for the lack of escape reaction is a missing signal, that cannot be a quality of the neck. As the motion pattern of the wing is obviously "strange" in these instances, we suggest that *Falco columbarius* is not "recognized as a raptorial bird" because an essential quality of wing motion is lacking in those cases. We also find (2) that the herring gulls (at Sjölunda) on many occasions react fugitively to an approaching *Haliaeetus albicilla* flying above the ice at a distance of more than an English mile in a direction towards the gulls, thus seen in the frontal view, the quality of neck being impossible to observe. Thus the conclusion is that the releasing signal is motional. We find (3) that harmless predators often cause escape, and (4) that some of these harmless predatory birds sometimes do not cause escape, although displaying the short neck as in hovering, and (5) we find that not seldom birds with a long extended neck but with an "eagle-like" flight cause escape reactions, whereas some non-predators with a short neck but a whirring flight and the merlin in "thrush flight" may not act as disturbances.

We may conclude that the motion pattern, and especially that of the wing is likely to play a part in "recognition" of raptorial birds.

The Ardeae are eagle-like in flight. 1 *Ardea*, 2 *Nycticorax*, 3 *Botaurus*, 4 *Haliaeetus*.

In this connection some few facts should be mentioned about the "arm test".

2. *The "arm test" an "eagle test"?* The mode of testing was chosen first for lack of economic resources for the experiments. Later it seemed advantageous to be independent of tools. There were also some other advantages—not only disadvantages when compared with experiments with models, dummies or other tools. Conditioned reactions were avoided to a high degree. Some special problems were available for study by this method of testing escape. Thus, for instance, the question of unity or not of the object for avian perception. It has, of course, also been of interest to complete the testing series in the same way as it was started. As has already been mentioned, a series of tests with models is planned by G. MARKGREN and the author.

Here we are mainly interested in the "arm test" as a possible "predatory bird model" test. Obviously the releasing signal when using the "arm test" is motional. But what is the "valence" of the motion? The experiments were performed at a distance beyond the critical distance for man, sometimes at more than one mile out on the ice, and the following observations were made. (1) Other "strange behaviour" elements do not arouse escape reactions at the distance, neither does "normal" activity. Boys may, for instance, play ice-hockey nearby or even throw things close to the gulls without causing escape reaction. Neither the "pumping" nor the running cause observable fugitive reaction. (2) The taking-wing reaction is reached when the test is made at a great distance only when performed in the frontal view. (3) The reaction is reached instantly during the second "wing beat". (4) The initiating motion pattern of the escaping gulls is the same as in escape reaction to an eagle and not to a man. (See above!) (5) The movements of the "arm test" are similar to those of an approaching eagle in frontal view. (6) Some small birds that do not react to an eagle if not very close, do not take wing for the "arm test", although they react to a man running—and occasionally to a

man throwing at a greater distance. (7) Until some better interpretation can be presented, the author would suggest that the escape-releasing effect of the "arm test" has bearing on wing motion in eagles and should be regarded as a motion with an "eagle valence".

3. *Hartley's test with motionless owl wings.* The results of the tests made by HARTLEY (1950) with "pairs of owl's wings, dried in an extended position and clipped together at the inner edges ..." are of interest for the discussion here. These wings of tawny owl and little owl were held motionless during the experiments. We might say that the birds in the test would experience an "owl" without neck, head and tail.

The result was a fairly high proportion of positive response with fear and mobbing reaction by the small birds.

In the discussion of escape reactions, the signal stimuli releasing escape, the escape releasers, have deservedly attracted interest, whereas the processes that prevent certain reactions are often overlooked. TINBERGEN (1951) has pointed out that "each instinctive mechanism is constantly primed, that is to say, prepared to come into action. Such a system can only work because blocking mechanisms prevent the animal from performing continuous chaotic movements." There is a certain principle of inhibition "between centres of the same level". At a low level of motivation some amount of "synchronous activity of two instincts" is possible. It may be, however, that there are still more complications. Some of the experiences in the field study have led the present author to the conclusion that many simultaneous stimuli to escape reactions are interacting either by summation or by counteraction, e.g. by blocking interaction. It is known that intraspecific blocking mechanisms inhibit extreme hostility actions in some socially living animals such as *Canis lupus* (LORENZ 1953). It may be that there are also "*inhibitors*", some stimuli preventing escape, although simultaneous escape-releasing stimuli may be present. What prevents escape, for instance, when ducks are fishing "together with" a *Haliaeetus* that is taking (their) fish in front of them? Or why do the ducks sometimes take wing for an eagle, whereas they will almost "ignore" the predator on another occasion? What makes an *Anser fabalis* that is on the wing and has been attacked by eagles charge resting eagles? If the short neck is a releaser of escape, is not then the long neck an "inhibitor" of escape? And, if it be so, what is learned and what is innate? Two different instincts may balance each other by blocking interaction. We know an escape reaction and perhaps an escape instinct. Could there possibly also exist a "non-escape reaction"? It may seem strange, but the present author has often been forced to think of it in that way in the field.

6. Some Properties of Hunting and Escaping Flight

At first glance, both attacking and escaping would seem to allow the acting birds much improvisation of motion. That impression will to a great extent be found incorrect. One of the primary motional tasks of the attacking predatory

bird is to make its motion curve interesect that of the presumptive prey in a si-
multaneous convergence. This convergence can be reached by catching up the
prey at a small angle between the motion planes (0°–45°) or by a pounce or a
swoop in an angle of 45°–135° between the flying planes of the two birds. The last-
mentioned behaviour is found occasionally in all raptorial bird species when
hunting birds (see above, cf. RUDEBECK 1950 B). If the hunter is attempting a
convergency, the hunted bird has to avoid the fatal collision. The goal of the
hunted bird may be reached in the case of intersecting or parallel motion curves
of the birds by means of a deviating motion and in the case of intersecting curves
by an acceleration and a simultaneous deviation performed as an *adjustment* of
its curve into a prolongation of the curve of the attacking bird. Such an adjusting
deviation has much in common with the adjustments to conformity of motion in a
flying bird flock. It is also possible and even probable that the motional adjust-
ments of bird flocks in flight and of both hunter and prey in an attack are innate
reactions of the orientation movement type (TINBERGEN 1951). Also RUDEBECK
(1950 B) has suggested that raptorial birds should attack "when the quarry has a
certain position in relation to the bird of prey". He also will assume the attack to
be a reaction automatically released at that moment (cf. TINBERGEN 1953). The
sort of escape flight that is directed as a distal prolongation of the motion curve of
the attacking bird is a typical moment of escape in most hunts with a considerable
extension in time and space. (It could be called "linear escape flight", "linear
flight" or "linear escape".)

A. *Linear (Escape) Flight*

Linear flying is a typical escape behaviour in some groups of birds when hunted
by predatory birds, namely, *Anser, Tadorna, Mergus, Gavia, Alca torda,* also *Sturnus*
and less pronouncedly in *Turdus* (especially in *T. viscivorus*). This behaviour is
found in some of our greatest bird species. It is thus typical of birds with a large
body, a large quantity of matter and consequently a considerable moment of
inertia. But in some cases it is probably not so much a question of the bulk of
matter and the inertia as of some anatomical properties, especially of the wings.
The species listed above are mentioned merely as examples. Thus the list is not
even an attempt at fullness. For a complete systematic list the birds have to be
discussed by species. Occasionally the behaviour in question will be found in most
big birds. Many of the small passerine birds, however, in no way deserve a place in
the list discussed, as they behave in another manner on escaping.

B. *Deviation (Escape) Flight*

The deviation of flight is found both in the final element of escape into a hiding-
place and as an alternating curve element of continuous flying escape. It will occur
either as single deviating movements or as continuously repeated changes of the
motion curve of the bird on escape.

(a) The single diving deviation ("the magpie escape")

Especially in the birds of the taiga zone there is often found an escape behaviour that seems to be an adaptation to the northern forest type. Over open fields such a diving motion will, however, look rather strange. The behaviour is found as typical in *Pica pica, Nucifraga, Garrulus, Perisoreus, Pinicola,* and to some extent in *Loxia, Bombycilla, Pyrrhula,* and *Lanius excubitor.* As the final part of a successful escape, a sort of diving deviation into concealing water and vegetation is often seen in *Anas crecca, A. penelope, A. acuta* and *Aythya ferina.* This behaviour means a motion curve very different from that of *Pica* and could perhaps be called the "teal escape". Some other final escape movements are mentioned below in sub-section C (cf. above Chapter III, Section 1 A).

(b) Repeatedly changing direction ("the goldcrest escape")

In birds with a minute bulk of matter we find an escape flight that seems some-what strange for a bird. It looks rather like the escape behaviour of many insects and especially that of the humble-bee. This behaviour can be described as a series of repeated changes of the flying direction. The rapid changes are performed in random directions with a strong vertical component and with the resultant curve describing a distal adjustment to continuous deviations from the direction of attack. This "goldcrest escape" may be successful even over an open field and even if the pursuer is the merlin. The predatory bird is obviously in these cases not helped by bulk and inertia. The "goldcrest escape" has been observed by the author especially in *Regulus regulus, Troglodytes, Parus caeruleus, P. ater, Muscicapa,* and less pronouncedly in *Luscinia suecica, Carduelis, Phylloscopus,* and *Sylvia.*

The list is here far from complete and much study has to be done in the field during the migration period of small passerine birds. There are, however, indications that the behaviour in question is found in small waders too. It should also be mentioned here that the merlin when hunting is at times seen to describe a motion curve somewhat similar to that of the hunted birds just discussed. Nevertheless the small bird may, by the behaviour just described, manage to escape from a small falcon, as mentioned above. Perhaps the optimal prey of a raptorial bird hunting over open fields is one not markedly smaller than the predator itself.

C. *The Final Moments of Escape*

At times the hunt is ended quite surprisingly by a deviating movement of the predatory bird itself, a sort of "animal factor". In such cases the motivation of the hunt may have been of a minor value. Mostly the successful escape is managed by the hunted bird by way of a deviating final movement into concealing vegetation or other structures or by means of an accelerated linear flight. It would perhaps seem as if this final movement of escape would allow a good deal of individual variation of behaviour, which is true, if minute details are discussed. The great differences in finishing escape are, however, found between species or groups of

birds not within the species. Just as expected, we find that the escaping bird is likely to choose its hiding-place in a structure with which it is familiar, as is also briefly mentioned above. The following varieties have been noted by the author:

(a) Escaping into concealing vegetation on the ground ("the bunting escape")

To hunting *Falco columbarius*, *F. tinnunculus* or *Accipiter nisus* attacking over open fields, some small birds frequently react by a deviating movement and succeed in hiding on the ground sometimes in poor vegetation. The predator may occasionally find the presumptive prey and start another attack with the same result. At times the small birds obviously run some yards before crouching. This behaviour is noted in *Calcarius lapponicus*, *Alauda arvensis*, *Eremophila alpestris*, *Motacilla flava*, *M. alba*, *Anthus*, *Oenanthe* and *Emberiza* (cf. Chapter III, Section 1 A).

(b) Escaping into water and/or ground vegetation ("the teal escape")

This behaviour has been mentioned above in the present chapter. It should be noted that the teal (*Anas crecca*) is occasionally seen to successfully escape an *Accipiter gentilis* in this way. The species involved have been mentioned above (Chapter III, Section 1 A). Very rarely the mallard is found to react thus or to make an attempt at this behaviour. Probably the small species of *Anas* are favoured by their ability to take water in a pliable manner. The waders found to act in this way are also mentioned above in Chapter III, Section 1 A.

(c) Escaping into higher and/or denser vegetation ("the tit escape")

If there is high and dense vegetation or trees nearby, most small passerine birds, when hunted, try to escape into that vegetation. The birds are likely to take the nearest way to a bush, a shrub, a tree, a bed of reed or even thick herbage by means of a sort of diving or slumping motion or an accelerated linear escape. It is the typical escape into a hiding-place. The behaviour is typical of tits, warblers, finches, the starling and some of the buntings. It is also chosen by the wood-lark, some pipits, the redstart, the robin and the goldcrest, if the vegetation is reachable. This hiding behaviour is found in pigeons and doves, too, (but very seldom seen in swallows). Some typical differences of habit are shown by the choice of hiding-place high up, near to the ground, near to the trunk or out on branches. These differences cannot be discussed here, as the discussion must be carried out by species. The most important aspect of the behaviour in question is that the escaping birds by their reaction have to manage an orientation both to the attacking predator and the hiding-place. Thus in this behaviour the aspect of escape as a motion from something to some other thing is well demonstrated. Somewhat related are the final moments of escape in a group of species adapted to climbing the trunks of trees.

(d) Escape into the trunks of trees ("the woodpecker escape")

When a woodpecker is attacked by a raptorial bird, it is seen to dart towards the trunk of a tree, where it starts climbing up the trunk spirally. If there are no

trees, the bird may be found to try an escape by ascending a telephone-post or a flag-staff or by darting against a wall to climb it, which may occasionally be fatal for a woodpecker. This special sort of behaviour will be found in *Sitta europaea*, *Certhia familiaris* and in *Piciformes*. In the open these birds are rather helpless when hunted. In *Picus* and *Dendrocopus* there is found a certain ability to dive in a deviating fashion, by which behaviour the birds are, however, likely to get too near the ground, because of the momentum of inertia.

(e) *Highly specialized escape behaviour*

Some species perform the final movements of escape in a very special way, probably as a result of adaptation to life in a special environment. Thus the wheatear, the snow-bunting and at times the ring-ouzel may be seen to escape into the rocks and hide among the boulders of the high mountains. An escape by means of a dart into the sea is, on the other hand, found in *Alca*, *Uria* and *Fratercula*, for instance. Here the dependence on the living habits of the bird is quite obvious.

D. *Physical Properties of Attack and Escape Flight*

As has been seen above in the present chapter, the final moments of escaping may show interspecific differences of a considerable degree. Nevertheless the possible varieties of motional curves of predator and prey are reduced to some few, if we regard the entire motion pattern of hunt and escape as being composed of individual and independent curves.

Using the terminology discussed above, we may sum up the question of possible motion curves of attack and escape in the following way:

(a) *Linear flight*

The motional curves of the attacking predatory bird and the escaping bird are approximately parallel to each other.

(a) The linear acceleration rate of the hunted individual is greater than that of the hunter. The escape will be successful.

(b) The acceleration rates are at the actual moments different or alike, but the raptorial bird is giving up. The hunt is finished without success.

(c) The rates of acceleration are alike or different. Thus the predator may be considerably swifter than the hunted bird. The latter, however, succeeds in escaping into a concealing structure (see (3) below).

(b) *Deviation of flight*

1. The rate of acceleration is greater in the motion curve of the hunted bird. The possible convergency point of simultaneously intersecting motional curves is actually not reached by an attack on the presumptive quarry. Instead, by an accelerated movement away from that point in a motional deviation of the prey and by the simultaneous effect of inertia on the predator in its attacking motion

curve, the distance between the birds increases beyond a critical value for releasing the hunting instinct in the raptorial bird. The hunt is thus finished.

2. The acceleration rate of the motion curve of the raptorial bird may be greater than that of the presumptive prey. Since the simultaneous convergency of motion curves is not reached, the great speed and inertia of the hunter works entirely in the direction of actually diverging motional curves out of the interspecific relationship enabling the hunt to continue. The hunted bird may escape into a hide. (See below.)

(*c*) *Escape into a concealing structure*

Regardless of difference in acceleration and speed, the hunted bird may, by means of the events outlined above in (1) and (2), reach a concealing structure in the environment or it may come in close contact with a crowded flock of related birds. To the hunting predator the hunted bird may then cease to act as a releaser of attack. The hunt will thus be finished and the escape successful.

7. The Question of Fear in Captured or Escaping Birds

The question, What are the subjective psychological realities experienced by the escaping bird? is not easy to answer. This question involves a discussion ranging from an anthropomorphic suggestion of a psychical activity in birds almost with a bearing on human thought, on the one hand, and fully mechanistic interpretation of the reactions, on the other. The opinions of excellent naturalists tend in either direction. For the sake of brevity we will discuss a few concrete questions on the problem.

A. *On the Interpretation of the Scream of a Captured Prey*

To start with a quarry in the claws of a raptorial bird, it is almost certain that the prey in that situation has a sort of mental trouble caused by the pain and obstructive encroachment upon its body. If not instantly killed, the seized bird is likely to scream (about a hundred observations by the author). That scream may to a certain extent be a mechanical effect of the compression of the thorax. And it may be a primitive expression of fear. Probably it has no or little warning power, nor has it any ability to prevent the predator from killing, but rather a stimulating effect in that direction. We may regard the death scream of a quarry as partly a mechanical noise, partly an expression of physiological pain and perhaps a mental affliction.

Although the author has never heard a prey screaming, the typical death scream when captured by its wings or *before* being seized, yet some ornithologists are quite sure that they have observed such instances. Any certain observations of that kind are of fundamental interest and should be published. (*A Corvus corax* in the claws of a female *Accipiter gentilis* screamed until the predator gave it up.) On the alarm note, see below.

B. *Hypothetical Fear in an Attacked Bird*

When predator and prey are whirling round in the open, their movements converging in attacks by the former and diverging in escape by the latter, the question of fear in the presumptive quarry is still more difficult to answer. However, it seems questionable whether the hunted bird in that special situation has a mental capacity for something more than the continuous flow of escape reactions. But if there is a "fear" or even a "death agony" in the avian consciousness in such cases, it should be noted that this possible fear does not often prevent a chain of very good escape manœuvres of deviation, acceleration or final hiding. And if there is no way of escape, the hypothetical mental affliction yet at times allows a defensive fight as long as there is any power of locomotion in the prey. Thus, if fear is evoked in the prey, it may be an activating fear. In our discussion we might consider the following.

1. We know from hunters that in a human being attacked by, or meeting with, a dangerous animal with the power to kill a man, there will be evoked a fear that is either an uneasiness activating and enabling defence or escape, or a paralyzing mental affliction. The man may cry out in fear.

2. Hunted birds are seen to take off in escape and try to hide but seldom to fight against the predator.

3. Also hunted birds or birds observing a predator are found to utter alarm cries (HARTLEY 1950).

4. The alarm note, however, is not to any greater extent than the escape movements an unmistakable demonstration of a mental agony of fear.

5. Observations of birds showing no escape reactions to an attacking predator cannot without question be adduced as evidence of "paralyzing agony of fear", as the cause of that inhibition of escape activity may be that the predator is detected too late for reaction.

6. Although there are no sure indications of a mental agony of fear in escaping birds, the question may be regarded as open.

C. *On Subjective Fear in Non-hunted Birds and Interpretations of Escape in vacuo*

Most instinctive actions are known also as reactions in the absence of adequate external releasing stimuli. They are in such cases regarded as "vacuum activities" (LORENZ 1937, TINBERGEN 1951). Even fugitive reactions are reported to take place "*in vacuo*" (KRÄTZIG 1940, POULSEN 1953). As to the interpretation, BIERENS DE HAAN (1937) has pointed out that the real cause of such a reaction may have been some unobserved external stimuli. In certain cases, however, as pointed out by TINBERGEN (1951), there cannot have been any external stimuli present as releasers of the vacuum activity.

To be brief, we find reasonable the following possible interpretations of "vacuum activity". (1) The reactions run seemingly *in vacuo*; there are unobserved external releasers ("pseudo-vacuum actions"). (2) There are no external (objec-

tive) stimuli. (3) There is an internal (subjective) reality acting as releaser and (a) that reality is a complex neurophysiological phenomenon of the brain, a conception or an imagination of the (external) phenomenon normally acting as the releaser of the reaction, or (b) the entire reality is a neurophysiological process of the reflection type without any corresponding imaginary phenomenon.

As regards the question of a hypothetical fear in non-hunted birds the current views differ somewhat. POULSEN (1953) suggests that animals are in a state of constant fear of enemies, almost as primitive people may be in fear of demons or as certain persons are afraid of darkness. He would also interpret the "akinese", the motionlessness of some animals, e.g. young birds, when attacked as an activity inhibition caused by agony of fear in a situation where escape is impossible. TINBERGEN (1951), however, in discussing "the internal factors responsible for the "spontaneity" of behaviour" without dealing in particular with the problems of fear and escape, has presented an interpretation of instinctive actions as rather automatic phenomena at the moment of performance. There may be little place for constant fear but perhaps for a continuous flow of impulses to all sorts of instinctive actions and also fugitive reactions, that are, however, blocked for chaotic discharge and only allowed to appear as responses to certain sign stimuli.

PART II

FUGITIVE BEHAVIOUR IN AVOIDING

DISTURBING CONDITIONS OR STRUCTURES

OF ENVIRONMENT

FUGITIVE BEHAVIOUR AS RESPONSE TO DISTURBING ENVIRONMENT CHANGES AND QUALITIES AND FUGITIVE REACTIONS IN MIGRATORY AND WINTERING BEHAVIOUR

Recapitulation and Introduction

In the previous section of this paper we discussed fugitive behaviour, (1) as reaction to signal stimuli of real dangers for the birds, (2) as reaction to phenomena of no danger to the birds and (3) as reactions released without any external stimuli (vacuum reactions). The question of possible subjective fear experiences in the bird was also discussed. It was suggested above that the escape reactions of fugitive behaviour should be regarded not merely as responses to an agony or fear in the bird, but as reactions automatically released out of the continuous flow of behaviour impulses by means of sign stimuli removing a blocking factor (TINBERGEN 1951) and taking place according to an innate pattern, typical of the species and the situation. Systematically, the behaviour is described with the characteristic releasing signals as a basis for discussion or according to type of activity. The single reactions are found to range from energetic bodily removal to mere orientation movements and down to non-locomotion, to escape *in situ*. There is nothing surprising in finding escape reactions in the avian intraspecific relations. Such reactions are found in sexual behaviour, especially when the presumptive mates are not yet familiar to each other (TINBERGEN 1951, 1953, 1958). Escape may probably also be traced in the run behaviour of mating (gallinaceous) females or in the submission attitude of females or young. But if we had not known the relationship of hunting and hunted, it would have been impossible to trace the quality of escape in such cases. The concept of "escape" without something to be avoided by the escaping subject would have been nonsense. "Escape behaviour", on the other hand, may obviously be put down as an action without avoiding single objects. Nevertheless, in treating the avoiding of some or other disturbing qualities of the (non-living and non-singular) complexity of surroundings, we should prefer to talk of "fugitive reactions". It goes without saying that here too, as regards the characterization, it should not be a question of subjective fear but just a sort of observable behaviour.

Both directly and indirectly, animal life is much dependent on climatic conditions, as is any mode of life (cf. ENQUIST 1929, AHLMANN 1949, MERIKALLIO 1951, PEITZMEIER 1951, KALELA 1952). It is thus to be expected that surviving animals should be sensitive to meteorological changes in the direction of harmful condi-

tions. It could also be expected that the surviving birds should avoid climatic conditions and meteorological changes that could be fatal to a non-responsive bird. In fact, the birds are found to respond more or less sensitively to "weather". There are well-known responses to both harmful and favourable conditions. Such behaviour is known and described as migratory behaviour or rather as elements of migratory activity. Migration is indeed not merely a simple response to weather, although weather elements play a great part in migration behaviour of many groups of animals.

For literature and discussion see SALOMONSEN 1938, WOLFSON 1940, 1952, 1954, ROWAN 1945, RUDEBECK 1947, 1950 A, DROST 1951, SCHÜZ 1952, CURRY-LINDAHL 1953, 1956, 1958, 1959 A, SVÄRDSON 1953, OTTERLIND 1954, KALELA 1954, HOCHBAUM 1955, and EDELSTAM & RAMEL 1956.

1. What Kind of Behaviour is Migration and Wintering?

A. *On Definitions of Migration Behaviour*

As is easily seen from the long lists of references in the papers just mentioned, ornithological discussion in our century has taken a considerable interest in migratory problems. The need to discuss definitions was, however, realized rather late. The "migration concept" is, however, a chapter heading in RUDEBECK (1950 A). (Important definitions of migration are also found in WILKINSON 1952, SVÄRDSON 1953, 1957, OTTERLIND 1954, HOCHBAUM 1955 and EDELSTAM & RAMEL 1956.) But as migration as behaviour is in fact not defined, we had better see how the term is practically used in modern literature and then try to find an arbitrary definition. A definition from an ethological point of view of the term 'migration' and of the migration concept is by no means an end in itself, since there exists an old and important ornithological tradition[1] outside the range of ethology, and the problems of migration have hitherto not been much discussed in the ethological literature.

A great part of avian activity may be put down as reproductive behaviour, whereas other groups of actions can be summarized as non-reproductive behaviour. Migration is part of the latter group (TINBERGEN 1953). Usually the reproductive behaviour is bound to a (cyclic) period of reproductional activity (cf. CURRY-LINDAHL 1958, 1959 A), during which period (different from species to species) there is not much migratory activity, with the exception of summer migration in *Apus* and fugitive (reversed) spring migration in (Palaearctic) *Passeriformes*, *Columbiformes*, *Charadriiformes* (mostly *Charadrii*) and to a lesser extent in *Anseriformes* and *Falconiformes*. (And foraging and diurnal flights; see below.) Migratory behaviour is thus found mostly outside the period of reproduction of the species and may be regarded as the most outstanding non-reproductive activity.

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[1] It is not an exaggeration to refer to "the ancient Greeks" here, since notes on avian behaviour in general or on migration are found not only in ARISTOTLE but also in HOMER, HESIOD, XENOPHON, etc. Avian migration is also mentioned in EXODUS XVI. 13, JEREMIAH VIII. 7, JOB XXXIX. 29.

Here we will begin with the classifications based on the annual cycle of seasons. At Falsterbo in autumn the birds are said to have migrated, when they have been seen to disappear in the southern quadrant over the sea.

(a) *Time of season as classification basis*

For the sake of brevity we will discuss the matter mostly from the Fennoscandian point of view.

1. *Autumn (or winter) migration.* An autumnal migration (in the wide sense) is usually the first demonstration of migratory activity in the life history of a bird. In Fennoscandia the phenomenon of autumn migration has been known since the time of LINNAEUS (cf. EKMAN 1922). As is pointed out by RUDEBECK (1947), the "autumn migration" in Scania may be *started* by the lapwing (*Vanellus*) already before the end of May. As a matter of fact, the last lapwings on "autumn" migration may, on the other hand, be seen in December or even January (MARK-GREN 1951 A). In *Anseriformes* the Scanian autumn migration has one early maximum in September, October and one later in December/January. Both maxima seem to be "normal" features of migration. Nevertheless, the behaviour demonstrated during those winter months could just as well be described as "wintering behaviour" (see below!). The birds show a tendency to remain on the spot regardless of weather (to some extent). On the other hand, the behaviour of these "wintering" birds in their "migrating *in situ*" is found to be grading into spring migration activity.

There is, however, a certain concentration of migratory activity in the months of August to October. Certain autumnal maxima are quite outstanding features of the migratory progress over Scania (Falsterbo, Sjölunda and Hälsingborg) and Öland (Ottenby).

The seasonal distribution of autumn migration is thus as follows (single extreme observations are not counted):

Gaviiformes. August–November, with a concentration of migrants to *September*.

Anseriformes.

Anseres (Anas). (August)September–November. Also here a maximum in late *September*.

Anseres (excl. Anas). The tendency is not quite pronounced, since the *diving ducks* at times winter in S. Fennoscandia and sometimes even further N. The published observations at Ottenby and Falsterbo, on the other hand, do not allow definite conclusions, although there are some indications that the crowding of diving ducks at Sjölunda in September/October also means a migratory maximum (another occurs in December/January).

Falconiformes. (July)August–November (December). Great maxima occur in September and October.

Charadriiformes.

Charadrii. (June)August–October(November). Some species show great differences in their migratory course from year to year. Most species however have a maximum in August/September (at times waders winter till *January* in Scania).

Columbiformes. There are outstanding maxima in *September–October*.

In *Piciformes*, *Apodiformes* and *Passeriformes* special conditions and interspecific differences make a summarizing conclusion rather difficult. Certain outstanding features, however,

should be mentioned: (1) the early migration (in June) of young *starlings* (*Sturnus*) and (2) the great bulk of small passerine birds on migration in *September/October*.

In conclusion, we find that there is a considerable concentration of birds on the move southward over S. Fennoscandia just in *September–October*. The term *autumn migration* thus seems well fitted to the observed facts.

2. *Wintering* and *winter vagrancy*. In discussing wintering behaviour there are certain aspects, which make it necessary to treat the matter below in another connection. Here we must continue to deal with *spring* migration.

3. *Spring migration*. In the bulk of Sjölunda observations from 1944 to 1958 it is quite clear that the spring migration has two maxima, namely, the one in March–Aptil, the other in May. It is also obvious that the spring migration may be started in the month of January or even December by *Corvus corone cornix, Alauda* and some other small birds. In the literature "spring migration" usually means migration towards a breeding territory. Sometimes the vernal migration is considered as the appetitive behaviour to the behaviour of the reproductive complex. Thus TINBERGEN (1951) says that HEINROTH (1910) "describes a still higher form of appetitive behaviour in mated ducks exploring the country for a nesting-hole. In extreme cases the appetitive behaviour may be prolonged and highly adaptable, as in the migratory behaviour of animals." This question will be discussed below.

As a matter of fact, the vernal migratory behaviour in southern Fennoscandia is often a sort of *oscillation* between motions towards the north and the south rather than a simple migration to the breeding place of the birds. If the migratory direction towards the nesting territory is thought of as the normal direction, then the movements back towards the south are defined as reversed migration. (See below; for literature on vernal migration, cf. OTTERLIND 1954.)

In conclusion, we find that, as regards the direction of resulting movement, the vernal migration is still more complicated than the autumnal migration. Not only are there pendulum movements diverging about 180° but also the extension in space and the prolongation in time is of the order of "reversed migration" at times. As regards the seasonal distribution, vernal migration may begin in winter but has certain maxima in March–May. "Spring migration" is thus a well-chosen term (cf. "Home migration" DROST 1951).

(b) Spatial extension and direction as classification basis

In the classical division of birds into three major types, the resident, the roving and the migratory types (BECHSTEIN 1805) a certain aspect of the spatial pattern of movements during the non-breeding period is taken into account.

MIGRATORS. The migratory type is thought to perform series of directed flights over an area considerably larger than the "home area". The direction may be merely a resultant direction.

ROVERS. Roving birds are thought to move about in random directions, whereas they are allowed to be on "migration" over great areas, sometimes, for instance, from northern Fennoscandia to Scania (*Loxia*). If they are roving in great num-

bers, they are usually regarded as "invaders" or as "irrupting populations". (The "irruption" means both an autumnal or winter or vernal migratory activity and a consequent change of range and number of breeding birds of the invading species.)

RESIDENTS. In the bird handbooks quite a number of birds are thought to be sedentary in winter. It is, however, questionable if there are any resident bird species to be found in northern Fennoscandia. An unpublished series of observations made by G. MARKGREN and the author from about the 15th of December to the 5th of January each year from 1938 to 1957 has given clear indications that any bird species to be found in northern Västerbotten during midwinter may be seen on the move. Observations made by Ö. ENARSSON in southern Lapland point in the same direction. Probably a real sedentary habit will be found only in populations of some few species. RUDEBECK (1950A) in his paper on migration has recorded migratory behaviour in many of the "resident" bird species, even *Perdix perdix.*

(c) Cyclic and non-cyclic characters as migratory classification basis

(1) *Migration with an annual cycle.* Migration with an annual periodicity is found in the "true migrants" mentioned above. For literature, see above (cf. also DROST 1951).

(2) *Migration with extra or non-annual cycles.* According to SILVONEN (1941) the invasion of *Bombycilla garrulus* should have a 10-year period (Grossinvasionen) independent of food, weather and other ecological phenomena. On the other hand, there should be also ecologically controlled interim irruptions (Zwischeninvasionen) in the waxwing. However, there may occur certain difficulties in saying what is Grossinvasionen and what Zwischeninvasionen (cf. RUDEBECK 1950A). SVÄRDSON (1957) has stressed the question of food supply for the irrupting bird species. Besides this he has pointed out the significance of an nonannual homing urge in the irruption species (cf., however, EDELSTAM & RAMEL 1956, HANSSON & WALLIN 1958). From the series of Västerbotten observations by G. MARKGREN and the author, the following facts may be considered. (i) Annual migratory movements are found in *Bombycilla, Carduelis flammea, Pinicola, Loxia curvirostra.* (ii) *Non-annual "invasion migration"* was noted in *Garrulus glandarius, Carduelis flavirostris.* "Irruptions" (in winter), in the sense of *sudden* occurrence of *great to enormous* quantities of birds, were found above all in *Bombycilla, Turdus pilaris, Carduelis flammea* and *C. hornemanni, Pinicola, Loxia, Parus ater.* (the black tit was seen on the 22nd of December, 1948, on the move in flocks containing *thousands* of birds). (iii) *Certain movements,* perhaps mostly local ones, were noted in *Parus cristatus, P. atricapillus, Picus canus, Dendrocopos major, D. leucotos, Corvus corax* and in *Lagopus lagopus.* (iv) *Resident habit* was found with certainty only in *Tetrastes bonasia.*

Summarizing, we find (1) that in Västerbotten and in southern Swedish Lapland there are not many species with pronounced sedentary habits, and (2) that in the non-resident species the limits between annually migrating birds,

rovers and invaders are undoubtedly very diffuse. CURRY-LINDAHL points out (*in litt.*) that the discussion above holds for the entire northern part of Norrland (cf. CURRY-LINDAHL 1946).

Hitherto we have discussed migratory behaviour in migration on a great scale as regards extension in both time and space. Before going further into migration problems dealing with movements of shorter duration and of less spatial extent, we should look at some more current bases of classification. The well-known and important fact that some species of Palaearctic birds migrate to the SE., whereas other species go in a (S)W. direction, is not significant for our subject and is consequently omitted as a classification.

(d) Sensitivity to external stimuli and differences of internal motivation as classification basis

The discovery that some birds in their migration respond more to internal factors than to external stimuli was of great value to the discussion on migratory behaviour. But the distinction between "Sommarfrischler" or "Instinktvögel" the "introvert migrants" and the "extrovert migrants" or "weather migrants" (Winterflüchtler) should not be drawn too far. External factors may be releasers in both groups. There are undoubtedly certain differences between these groups, although the individual intraspecific behaviour difference might mean overlapping. As a matter of fact, regardless of species, any migration is to some extent controlled by internal and external stimuli, whether it be a diurnal or nocturnal migration and regardless of season. The basis for division of the above-mentioned groups of migrants is not entirely the same in all cases. There is, however, the aspect of sensitivity to external stimuli common to them all. For discussion and literature, see PUTZIG 1939, ROWAN 1945, SCHÜZ 1952, SVÄRDSON 1953, WOLFSON 1954, OTTERLIND 1954, EDELSTAM & RAMEL 1956, CURRY-LINDAHL 1958.

(e) Diurnal rhythm as classification basis

The division of migratory birds into two major groups, (1) the *diurnal* migrants and (2) the *nocturnal* migrants, has a bearing on the important problem complex of activity rhythm. Here the normal avian activity rhythm curve, as well as the rhythm of migratorial activity—both the diurnal and the long-time rhythm—has to be considered. In this paper we shall not discuss the long list of references on the physiological and ethological problems concerning the rhythmic functions of migration. ROWAN (1946) made experiments with artificial light in order to test the significance of daylight for the sexual and the migratory cycles. PALMGREN (1949) tested the actograph curves of cage birds as to their significance for conclusions on the activity of wild birds in the field. SCHIELDMACHER (1938, 1939, 1952) and WOLFSON (1945, 1952) in different ways have carried ROWAN's experimental work further. At present the anterior lobe of the pituitary and the activity of the hypothalamus in hormonal processes seem to be of most interest in this connection.

Regardless of the physiological function of increasing and decreasing migratorial motivation in the bird, it is interesting that there are certain external factors which act as releasing stimuli, and especially in cases, in which a nocturnal migrant is in some way incited by external stimuli to day migratory activity. Of no less interest is the opposite change of activity, that from diurnal activity to nocturnal migration activity.

As pointed out by PALMGREN (1949), nocturnal migration seems to be carried out mainly during the early part of the night. On the other hand, the migration activity of birds wandering in daytime has a pronounced morning maximum (PALMGREN 1949, RUDEBECK 1950).

Fusions of diurnal and nocturnal migratory habits were observed by the author in some 400 different cases. They are grouped according to the following classification.

1. *Pronounced migration* by birds with the habit of daytime wandering from late evening to about midnight in spring or in early autumn in northern Fennoscandia (cf., for instance, MARKGREN, 1951 B). It has to be mentioned (a) that the nights are then rather light and (b) that an induction effect is here noted at times (cf. OTTERLIND 1944, 1954).

2. *Pronounced morning migration* in *nocturnal* migrants occurring in calm and stable air masses (cf. MARKGREN 1955).

3. *Pronounced reversed daytime migration* in nocturnal migrants carried out in adverse weather conditions in spring (see the tables; for literature, see below on Reversed Migration).

It has to be stressed that the most important point of our discussion above on groups of birds with daytime or nocturnal habits of migration is the fact that both groups are in their migratory behaviour controlled by an internal rhythm as well as by external factors (cf. CURRY-LINDAHL 1958, 1959A). This will be of most interest for the discussion of fugitive elements in the migratory behaviour. Before leaving this part of the present chapter, a few words may be devoted to the subject of activity-rhythm study. Obviously, in the study of certain activity rhythms in animal migration, we will find a point at which experimental physiology, anatomy, histology, comparative ecology and ethology have to join with close field study, and where also the numerous skilful amateurs can do valuable work by careful observations. The problems in question are likely to play a great part in the future in the work of institutes and field stations for study of avian migration.

(*f*) *The migration classification suggested by Wilkinson*

The migration behaviour we have hitherto treated is entirely of the sort that is defined by WILKINSON (1952) as anastrophic migration (anastrophic from Greek ἀναστρέφειν, here meaning "to turn (oneself), to return"), the autumnal and vernal migration to and from the breeding grounds or the birthplace. On the other hand, all other migratory movements are put down as diasporic migration (diasporic from Greek διασπείρειν, here meaning "to spread, to scatter about",

German "ausstreuen, verspritzen"). The term "diasporic migration" is thus synonymous with the "interim migration" or "between-migration" (Zwischenzug) adopted by GEYR VON SCHWEPPENBURG (1943). In the diasporic category of migration should be placed the winter movements, the "weather flights" in swifts (KOSKIMIES 1950), the moult migration and the juvenile vagrancy. On the latter phenomenon some few facts of importance for our discussion should be mentioned.

(g) Juvenile vagrancy

Under this heading are included some facts and conclusions on juvenile migrations, mainly in Ciconiiformes. We will confine the discussion to records of these birds in Sweden, mentioned in systematic order.

(1) ARDEAE

Ardea cinerea. In late summer and autumn both juvenile and non-juvenile herons are found outside their birthplaces and breeding grounds. There are a fair number of undated finds of the species in Västerbotten, Norrbotten and Swedish Lapland. The present author also has observed *A. cinerea* in Västerbotten (cf. OLSSON 1958).

Ardea purpurea. Of seven certain finds of the species in Sweden, two may have been adult birds.[1] (One bird shot at Hisingen in Bohuslän on the 18th of November 1882; one bird shot at Tutaryd in Småland on the 13th of August, 1912.)

Egretta garzetta. This species has been found at least twice in Sweden. In both cases birds with elongated crest plumage in late spring (14 15 May, 1949; 5 June, 1952) were concerned (see RAMEL 1950, LUNDHOLM 1952). Probably both finds are to be interpreted as prolonged migration (cf. OTTERLIND 1954).

Egretta alba. This species has been reported seven times with certainty in Sweden. Adult birds, however, are not recorded.

Nycticorax nycticorax. One young bird was shot on the 11th of November, 1863, at Silvåkra in Scania and on the 14th of October, 1907, another young bird was shot on Skaftö in Bohuslän.

Ixobrychus minutus. Of this species young birds have been found in Sweden on four occasions, three of them in autumn.

(2) CICONIAE

Platalea leucorodia. The spoonbill has been recorded five times in Sweden between 1928 and 1956. Two of the finds were made in autumn in Västerbotten and Lapland. In one case it was an adult bird (14–16th May, 1956, at Skanör in Scania).

Plegadis falcinellus. The glossy ibis has also been found five times in Sweden. One record is from September. One of the birds was an adult. (For literature on

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[1] OTTERLIND has pointed out that one-year-old specimens of *Ciconiiformes* may wrongly have been defined as adult birds (verbal comm.).

records of these species in Fennoscandia see S. NILSSON 1858, CURRY-LINDAHL 1947, LØVENSKIOLD 1947, MALMBERG 1950, OLSSON 1958).

(3) SUMMARY AND DISCUSSION

The above-mentioned *Ardeae* and *Ciconiae* are known for their juvenile wanderings in "random" directions. As is seen above, however, there are also instances of similar movements of adult or one-year-old birds both in spring and autumn. Nevertheless we have to recognize a juvenile migration differing from that of the adult birds in direction and extension. It is typical in the species mentioned, and also in *Sturnus* (SVÄRDSON 1953) and in *Larii* to some extent (OTTERLIND 1948. 1954. OLSSON 1958). This sort of migration may play a part in the dispersal of a species to new biotopes (OTTERLIND 1954). The juvenile wandering also is thought to be "an important factor in the homing orientation of the following spring" (THORPE 1944). At times this migration is mentioned as "undirected" (KALELA 1954). According to current opinion, these juvenile wanderings are not true migration. For the purposes of the discussion we consider the juvenile migration in late summer or autumn. The following cases occur:

(i) Juvenile wandering conforming (and contemporary) with the specific autumnal migration. The behaviour will be described as "normal" migration.

(ii) Juvenile wandering neither conforming nor contemporary with "normal" autumnal migration.

> (a) There may be a resulting direction with a great extension. That direction may:
>> (1) Conform with the "normal" vernal direction.
>> (2) Not conform with any "normal" migratory direction of the species.
> (b) There may be no resulting direction with a great extension. The behaviour is then similar to that of a resident bird, if the extension of the resulting movement falls within the specific breeding grounds. Cases (i) and (ii) (a) are described as migration behaviour, whereas case (ii) (b) may be described as "undirected movements". Cases (i) and (ii) (b) may be survival. The typical juvenile migration seems to be the response to a strong internal motivation rather than a reaction to external factors.

Before going on to discussion of fugitive behaviour in migration and wintering we have very briefly to discuss the definitions of wintering, of "reversed migration", and the definition of the migration concept.

B. *On Definition of the Wintering Concept*

In most ornithological handbooks, as, for instance, "The Handbook of British Birds" by WITHERBY *et al.*, the term "wintering" and its synonyms are used in the following senses:

1. The sojourn of a bird anywhere outside its breeding ground during the winter season. It may be summer, in the place where the bird is actually on the move. Thus the arctic tern (*Sterna paradisaea*) "winters in southern ocean and on coasts of Antarctic Continent" (*op. cit.* V: 38).

2. The sojourn of a bird in a territory during its winter season. For example, the Iceland gull (*Larus glaucoides*) "winters south to Scandinavia, Faeroes, Iceland, Great Lakes, Long Is. ...." (Witherby *et al.* 1952).

3. The stay of a bird during the winter in a territory, when the climatic and meterological situation has a quality of winter. The birds may be "resident", like the Scottish ptarmigan (*Lagopus mutus millaisi*): "In winter ordinarily remains at considerable elevations, but may be temporarily driven down to lower and more sheltered corries by blizzards and quite exceptionally even to level of cultivation." (Witherby *et al.* 1952.) Or the bird may be "occasionally staying winter", like the quail (*Coturnix coturnix*) (WITHERBY *et al.* 1952).

C. *Migratory Movements in Wintering Birds*

As is seen from the above-mentioned instances, the wintering birds are not quite resident in their wintering. That wintering birds are on the move was suggested by RUDEBECK (1947). Later on, such migration on wintering grounds was proved during a South African expedition (1950–1951) especially regarding terns, waders and swallows. The food supply seems to play a great part in these migrations on wintering ground (RUDEBECK 1953).

RUDEBECK (1947) also pointed out that migration movements are seen in several species in Sweden during the winter. "Several birds can be induced to migrate southward, if the weather is suddenly getting cold. The birds "escape the chill." Heavy ice formation or decreasing food supply may have a similar effect." (Op. cit.; the original is in Swedish.) Movements in wintering birds were discussed by DROST (1929).

For the sake of brevity we will summarize what is known on the subject.

1. Wintering birds in all three senses (above) are found to be on the move for food (cf. RUDEBECK 1953; cf. also the literature on invasions in SVÄRDSON 1957).

2. The birds are found in motion in the "normal" direction of their autumnal migration in favourable weather (cf. RUDEBECK 1953).

3. The direction may be that of the vernal migration (especially in *Corvus corone cornix* in Scania from December to January).

4. The direction may be different in different flocks, towards S., N. or E. (especially observed in waders like *Vanellus* and *Charadrius apricarius* in November and December in those years when great crowds of waders make attempts to winter in Scania, as in 1951, 1953, 1958).[1]

5. The birds are seen on migration in the autumnal direction in bad weather,

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[1] Usually these waders have left the Löddeå and Sjölunda area before the end of December. Last inland flock of *Vanellus* in 1958 was seen on the 24th of December near Ringsjön in Scania.

just as in the reversed migrations in spring. Often such catastrophic (fugitive) migration will be the end of an attempt at wintering in southern Fennoscandia.

6. Some species when wintering are found rather resident (*Emberiza calandra*, some owls like *Asio flammeus*, certain eagle individuals, amongst others) (cf. RUDEBECK 1953).

7. For the period of 1949–1958 the author has studied the correlation between attempts at wintering in Sjölunda and weather elements. The following conclusions have been made:

(i) The temperature is of significance, both as regards amplitude and fluctuation.

(ii) The value of insolation is of a certain importance.

(iii) "Hidden" temperature factors may play a part by wind and humidity.

(iv) For late warblers, swallows and swifts the air masses seem to be of importance (an indirect weather factor acting by controlling the food supply).

(v) Mostly it is the birds confined to the seashore, that (in the sense of subsection B (2)–(3)) are making attempts at wintering, thus waders, ducks and some passerine birds. (The author has made an analysis of weather and vernal migration from 1946 to 1957. Although the material will be published in full later on, it should be mentioned here that there is a quite obvious interrelation between the weather situation, *in toto* of western and central Europe and the run of vernal migration in Scania.)

D. *On Discussion and Definition of Reversed Migration*

(a) *Autumnal migration*

As was pointed out by RUDEBECK (1943) the normal migration in autumn is by no means a simple motion in one single direction. At Ottenby or Falsterbo the birds are seen to leave and return, to describe almost circular movements, make an "attempt at" migration and return repeatedly (cf. RUDEBECK 1943, 1950 A).

The autumnal migration at Falsterbo may thus be said to be composed of:

(1) Movements in the southern quadrant. "Normal directed" migration; "true migration."

(2) Movements starting in the southern quadrant, turning clockwise or counterclockwise into the northern quadrant.

(3) Movements entirely in the northern quadrant.

As is shown by RUDEBECK (1943, 1950 A), the winds, their direction and rate, the (thermal) upwinds and the visibility play a part in the behaviour of the birds on autumnal migration at Falsterbo.

2. *Vernal migration*

Also in vernal migration there occur movements in opposite directions, thus at Falsterbo or Sjölunda towards N(E). and S(W). There is, however, a certain

difference between autumnal and vernal migration, viz. the effect of temperature upon choice of direction of movement. Both in spring and in autumn the temperature seems to be a proximate factor for releasing certain migratory behaviour, but whereas a cold spell will cause southward movement in autumn and spring or at least act as a blocking factor in spring, and warm air will give rise to homing movement in spring, yet in autumn the warm air does not cause northward flight (for discussion and literature, see SVÄRDSON 1953).

The phenomenon of the *reversed direction of movement* has been known for a long time. For discussion, cf. DAHL (1938), who made some observations first on reversed and then on normal spring migration at a locality on the Swedish west coast. He suggests that the anomalous movements may have been released by a cold front with snow over the inland areas. The direction of the wind seems to have played no part. Similar cases are mentioned by MALMBERG (1945) and SWANBERG (1948), who assumed a psychical effect of the snowfall. BERGMAN (1949) was also of that opinion. SVÄRDSON (1953) discusses some cases of reversed migration. He objects to the interpretation of SWANBERG. In all the cases mentioned the "normal" northward migration has for one day or several days been changed into real migration south or southwest, obviously influenced by cold fronts (and snow), at times also by strong winds. It has been reversed migration released by weather change.

As is seen from the present author's lists, temperature, wind and snowfall all play a part in releasing reversed migration. The correlations are discussed below.

Before discussing the fugitive reactions in (reversed) migration and some other behaviour we will, however, consider the term migration. For literature and current use of the term, see above.

E. *On Definitions of the Term Migration*

First, two important statements should be quoted here: "... there is no difference in principle between real migration, movements taking the form of irruptions, and the autumnal restlessness seen in non-migratory birds and actually resulting in migratory movements taking place over short distances varying between 500 m and 10–20 km, a sort of 'miniature migration'." (RUDEBECK 1950 A.) "Apart from these migrations, the Herring Gull shows daily movements to and from its social sleeping grounds. Thus the Herring Gull shows clearly how many types of directed flight there are in birds. The most extreme type is usually singled out and called "migration", but this obscures the fact that "migration" is only an extreme case of directed movement, differing in degree only from such phenomena as flight to the sleeping places, return from the shore to the breeding colony, or flight to the feeding grounds." (TINBERGEN 1953.)

(a) *Discussion*

These two statements are made in the knowledge that there is nothing mysterious, nor even extraordinary, in avian migration, that the birds are not re-

corded as residing, although breeding somewhere. Obviously the authors quoted have the migratory behaviour in mind, not the purpose of migration or the releasing factors. This point of view is quite necessary in attempting a definition, unless we want, in time, to amass an abundance of definitions of migration based on proximate releasing factor, "purpose", number of birds in action, spatial extension, and so on. We should keep to what is common in migration behaviour and to what is observable. The discussion above has mainly been confined to the wide-ranging migration that may be put down as the most outstanding phenomenon of the non-breeding period. Here we have to define migration also as regards diurnal and foraging migration, phenomena that do not exclude the reproductive activity.

The following points are of importance for the definition:

(1) Avian migration appears as (mostly) flights of a certain period dependent on the diurnal or seasonal shift or the tidal rhythm and is characterized by an observed activity rhythm in the bird corresponding to the planetary rhythm.

(2) In certain cases physiological changes with a period corresponding to the action period and/or the astronomic rhythm is stated (see above).

(3) The planetary rhythm, in causing periodic environmental changes, at times accentuated or, on the contrary, obscured by non-periodic changes which have a bearing on food, shelter, weather elements and climatic conditions.

(4) The birds have proved to be highly dependent on (responsive to) the changes mentioned in (1)–(3).

(5) There are certain interspecific and intraspecific differences in length, spatial arrangement, intensity duration, and constancy of action of the flights.

(6) A homing behaviour with a bearing on "Ortstreue" is at times found to coincide with the final moment of both vernal and autumnal flight.

(7) An initial or increasing mating behaviour is sometimes found to overlap the vernal flight behaviour (cf. CURRY-LINDAHL 1958).

(8) In certain species (*Corvus monedula, Cygnus, Anser*, amongst others) the relationship of mating is not extinct in the space of time between autumnal and vernal flights.

(9) Homing and/or mating or activating or even decrease of sexuality may play a part in internal motivation of the flights.

(10) Any kind of flight may, on the other hand, be found without an observable connection with homing or mating.

(11) Simultaneously overlapping behaviour or elements of behaviour (see (2), (6)–(9)) should not be regarded as the consummatory act of flights, which were the appetitive behaviour of, for instance, homing or the entire complex of the reproductive instinct.

(12) Mating, homing, hunting, escaping or other behaviour may actually be in a positive or negative interrelationship to the flights (see above; cf. RUDEBECK 1950A, EDELSTAM & RAMEL 1956).

(b) *Definition*

Avian migration is the (mostly) volant response partly to spatial distribution of mainly food and shelter and partly to periodic environmental changes caused by the planetarian rhythm, at times accentuated, or, on the contrary, obscured by non-periodic modifications, which changes act as behaviour releasers (in a wide sense) in the bird, in which a corresponding (physiological) rhythm may be found.

As is seen, the migration is thus interpreted as a progressive adaptation in birds to life under changeable conditions. The primary ethological question, however, is not interpretation but description of observed facts.

(c) *About information on migration*

Information of any kind on avian migration could thus appropriately be given by records of the following facts: (1) number and species observed, (2) time of observation, (3) observation locality, (4) spatial properties such as directions of motion and heights, (5) characteristic features (and/or general impressions), (6) details of behaviour, (7) known ecological conditions such as food supply, weather elements and weather situation. Notes from the field are sometimes lacking in facts that could certainly have been added, increasing the value of the report.

F. *Some Characteristic Behaviour Elements in Migration*

According to the discussion above, there is nothing surprising in finding a great variety of behaviour elements overlapping the migratory pattern. Certain reactions, although they would not as isolated phenomena be held to be unmistakable indications of migratory activity, should notwithstanding be entered as characteristic features of observed migration behaviour. In this connection two different groups of behaviour elements should be mentioned:

(a) *"Addictive" behaviour in migration*

The term "addictive" is used here to indicate an activity in which the bird shows something like an "addiction" to a phenomenon. In other words, the migrating bird is in a positive way reacting sensitively to these phenomena, which are in a wide sense working as releasers of the "addictive" behaviour. Although the matter has to be treated comprehensively later on, some few examples of these releasing phenomena and the reactions to them are to be mentioned here.

REACTION TO THERMAL UPWINDS

(1) In *Falconiformes*. The eager soaring of most raptorial birds is well known to any ornithologist of Fennoscandia. As part of migratory behaviour it is treated especially by RUDEBECK (1943, 1947, 1950 A, 1950–1951, 1953).

(2) In *Charadriiformes*. (i) *Charadrii*. By the present author "addictive" reaction, including soaring on thermal winds, has been observed occasionally in many of

the wader species and, above all, in *Numenius* and *Limosa*, also in *Vanellus* and *Tringa* (cf. MARKGREN 1951, 1955A, 1956). (*ii*) *Lari*. Such reactions in some species of *Larus* over Ottenby are mentioned by SVÄRDSON (1949). By the author, observations of this behaviour have been noted also in *Stercorarius longicaudus*. (*iii*) In *Passeriformes*. "Addictive" reactions to thermal upwinds are found in connection with migration in *Corvus* (all of the Fennoscandian species) (cf. CURRY-LINDAHL 1951), *Pica, Nucifraga, Plectrophenax* and, surprisingly enough, in *Parus* and *Passer*. (Observations of the reactions in *Alauda* and *Anthus* are somewhat questionable, as a similar behaviour is a typical element of song behaviour. In swallows similar behaviour is observed in connection with autumn migration up in the high arctic mountains of northern Fennoscandia. Here reaction to food concentrations, however, is often involved (cf. BRINCK & WINGSTRAND 1949). Insects of different kinds from the woodland were scattered about on snow fields in the mountains, probably by upwinds.) It should be stressed that this behaviour is found in all months of the year and in different air masses but above all in unstable masses of the type mPK and cPK (cf. BLAIR & FITE 1957; LUDLAM & SCORER 1957).

REACTIONS TO DYNAMICAL UPWINDS

In the rapid motion of air masses, dynamical upwinds are created in connection with hills and mountains. A typical "addictive" reaction to such currents is found in eagles, *Circus, Falco tinnunculus, Buteo, Larus, Stercorarius, Corvus corax* and *C. frugilegus*. Of special interest are observations of birds such as buzzards and rooks when they are seen to deviate from their "normal" migration direction about 90° by following an escarpment on reacting to such upwinds. It should be pointed out that false impressions of effects of "leading-lines" or even "leading points" (GEYR VON SCHWEPPENBURG 1929, 1933, 1949) may be obtained by overlooking the outstanding phenomenon of "addictive" reactions to thermal winds and to eddies and upwind currents generated in horizontal air flow against obstacles. These effects are easily seen in the high mountains as well as on the hills, mountains and coasts of Scania. It was also observed by the author at the low escarpment of the Scanian island of Ven and, occasionally, at the western low escarpments of the two great islands of Öland and Gotland. In order to avoid misunderstandings, we shall summarize a few points on "guiding-line" effects caused by "addictive" reactions (or "addiction" behaviour). There are also fugitive elements to be found in these guiding effects. Both may act simultaneously (cf. VLEUGEL 1943).

"ADDICTIVE" BEHAVIOUR IN GUIDING-LINE AND GUIDING-POINT EFFECTS

The definition of "Leitlinie" as given by GEYR VON SCHWEPPENBURG (1929) will be presented here translated into English by RUDEBECK (1950A): "Guiding lines are mostly narrow and extended geographical-topographical features in the surface of the earth, whose special properties cause the migrating birds to fly

along these lines. The bird is influenced by them choosing its migration route, it is to a greater or lesser extent *guided* by these lines." RUDEBECK points out that "the most effective guiding influence is exerted by a straight and unbroken coast-line of a big lake or sea, especially if it runs at a certain angle with the main direction of the birds reacting upon it". He suggests that "many reasons could be advanced to support the opinion that the best guiding-line effect is achieved if this angle between main direction of migration and guiding line is 45–70°. However, the general topography of the landscape, the length of the guiding line, the areas previously overflown, and probably also other factors contribute to complicate the effect." Obviously, the main point of that discussion is an avian reaction to optic stimuli.

(1) *Reaction to optical stimuli.* RUDEBECK (1950 A) has stressed the effect of the morphological features and the ecological significance of the contrast between land and water. MALMBERG (1955) has pointed out the effect of such ecological properties of inland areas as woods, cultivated plains and mountains. He has also stressed the significance of *"leading-points"* like "small islands as Heligoland or inland wood or mountains on a plain, …". We could for brevity call this effect the *"insular effect"*.

A certain reaction to the view of an island is found when the migrating birds outside the reach of meterorological influences from the island are deviating towards it. This behaviour has been observed occasionally at Måkläppen, Ven, Hallands Väderö (in Scania), on some small islands near Kågnäsudden (Väster-botten) and at Vardø and Hornøy (NE. Norway). To nocturnal migrants on the move on calm nights before sunrise this effect might be of importance.

(2) *Reaction to meteorological stimuli.* (a) *Thermal stimuli.* An effect of thermal influences might be obtained in the upwinds. (No observations.) (b) *Upwind stimuli.* See above on reactions to upwinds. TINBERGEN (1953) states about the herring gulls: "The concentrated movement along the coastline is due entirely to the up-draught there with a westerly wind. At all seasons, gulls have an amazing capacity of finding the upcurrents, even in quite irregular dune country." In these reactions we have "leading-line" effects in the current sense, as is seen from one example. In September and October, 1954, and October, 1955, the author had had the opportunity of checking the migration over the island of Ven on some days with good migration activity. The winds were from NW. to SSW., mostly from (S)W. (never from the E. quadrant). Small passerine birds, *Corvus frugile-gus*, *Buteo* and seldom *Pernis*, *Pica* and *Garrulus* were taking their way over or partly around the island. The rooks and buzzards reacted eagerly to upwind currents, whether thermal or mechanical. Of most interest were the birds that first migrated along the Scanian coast, then turning clockwise S. of Ven took their course towards the S. part of the island (reaction to optical stimuli, "insular effect"), from where they followed the western escarpment of the island to its northern point, where they again returned to a (S)W. migration. Thus the deviations caused by the island amounted to 110–120° from the original course.

(*b*) *General remarks on fugitive behaviour in migration*

The fugitive elements of migratory behaviour have now and then been mentioned in the discussions above. They are outstanding features of behaviour in wintering birds. They are also seen in the autumnal avalanches induced by fall of temperature (SVÄRDSON 1953). Above all, the fugitive moments of behaviour are found in reversed migration (see above). Just as one group of reactions characteristic of birds on migration is that of the addictive behaviour, so the other main group is that of fugitive behaviour. Obviously, these groups of reactions, without being the migration behaviour itself, control or balance behaviour of the migratory pattern. The relationship of these reactions in wintering and migration deserves a comprehensive treatment. A few instances of addictive reactions have been briefly discussed above. Others are just touched on. Reactions to food concentrations are mostly thought not to be of significance as proximate factors in migration (cf. SVÄRDSON 1953). Probably, however, they are, in some irruption migrations (cf. SVÄRDSON 1957) and sometimes in wintering birds (cf. RUDEBECK 1953). They certainly are proximate factors in foraging migrations (TINBERGEN 1953).

Below, however, having discussed the fugitive behaviour as reaction to "danger individuals" and "danger phenomena" ("disturbers"), and having briefly outlined what has to be regarded as wintering and migration, we should now discuss the fugitive reactions found in the activity complex of migration and wintering. It should also be pointed out that this second section is at the same time the introduction to the treatment of the main body of observations made by the author from 1938 to 1958.

2. On Fugitive Behaviour Elements of Response to Weather in Birds on Wintering and Migration

Introductory

"Wintering" here is used in the sense defined in subsection B (2) (3) of Section 1 above. For discussion of migration see that section.

Among climatic and meteorological factors the temperature is usually thought to be of special significance for vertebrate animal life. Unfortunately the thermic conditions of animal life in the field, and especially those of life near the ground, are not well known, except where microclimatic research has been carried out. (For discussion see GEIGER 1957.) Of special interest are observable changes of temperature and simultaneously observed avian behaviour. The bird on migration will meet thermal change as a function of time or space. Falling temperature may be registered as a long periodic or a sudden negative change of the diurnal mean value, without or with a contemporaneously decreasing amplitude. A steady drop in temperature with a little range between diurnal minima and maxima is typical of the maritime winter, whereas a large diurnal amplitude will be found in the winter of continental climate areas. (On microclimatic conditions

see GEIGER 1957; for discussion of hygric continentality, see also GAMS 1931–1932.) In our discussion we have to distinguish between temperature as a physical quality of environment and the physiological temperature, the avian "temperature experience".

A. *Fugitive Reactions to Fall in Temperature*

As was pointed out by ENQUIST (1924, 1929), the extreme values of temperature are likely to play a great part in the conditions of life. It is thus also probable that surviving animals should respond to these extreme temperatures (cf. also above). Nevertheless we have to discuss also the means of thermic condition and what is known of avian response.

(a) *Reaction to temperature as isolated weather element*

Above it has been mentioned that thermal effects are hidden in the factors of wind and humidity. These effects are physiological (see below). Here we will first consider the drop in temperature as a statistical property of thermic intensity of environment, air, water and ground.

(b) *Reactions to long periodic change*

"Long periodic" here means extra-diurnal to seasonal. It is a fact that winter weather in high latitudes is obviously dependent on air masses. They are likely to accentuate or counteract the seasonal tendency or just to balance on the mean (latitudinal exchange).

STEADY DROP IN TEMPERATURE

In late October to December there is in Scania a steady temperature decrease, also in the case of mT air invasions of long duration. Advection clouds and fog, however, are likely to restrict the cooling process and to limit the amplitude. The drop is retarded. A similar effect is obtained in mT or cT masses in winter high-pressure situations with feeble winds.

Observed reactions. Gradually the foggy situations may change into steady cold and cloudy weather with a decreasing temperature about zero. If the foggy period is characterized by little avian activity, the same must be said of the colder period with overcast sky. Only rarely are migratory movements actually observed. But there is nevertheless a steady decrease in the number of resting birds on the inland waters and a simultaneous increase of resting birds at the coastal localities, such as Sjölunda. That is typical of an early period with an absolute increase in number of birds at the coast. Later on, in late November and December there will also appear at the coastal localities an absolute decrease in the numbers of resting birds. At that time a certain fugitive behaviour is observable in the birds, a sort of "escape *in situ*". The birds, *Larus*, *Anas*, (*Anser*), *Cygnus* (late waders and passerines) are found to react with sleep, often crowded together very tightly and orientated sensitively with heads pointing into the (often slight) wind (see below).

Summing up, we find in these conditions (1) a slow migration from the inland areas towards the coastal localities, mostly observable as a contemporaneous change in number of birds, occasionally seen in actual movements, (2) a slow SW. migration away from the coasts, at times directly observed break-ups, (3) "head-to-wind attitude" (Swedish "motvindsattityd") and sleep during the coldest parts of the day. Often there are great crowds of birds tightly packed together in a sort of "escape *in situ*". The behaviour is thus a slow adaptation with some fugitive quality.

ALTERNATING DROP AND RISE IN TEMPERATURE

The rising temperature may be the result of a change in air transport or just a slight subsidence.

Observed reactions. For some years the author in the autumn made excursions three times a week from Lund to Sjölunda or to some of the inland lakes of southern Scania. The most outstanding feature observed there was an inland movement, a migration from the coast towards the inland waters during the warmer periods.

(c) *Reactions to short periodic or sudden changes*

With an influx of cPK or mPK air masses, often with a pronounced cold front, a considerable drop in temperature, especially of the (nocturnal) minimum value, is likely to occur. As there is usually in these cases a clear diurnal rhythm in cloudiness, a corresponding rhythm in the course of the temperature is also found. The nights may be very cold, whereas midday before maximum cloud formation may be rather warm. The whole meteorological situation tends towards continentality.

STEADY DROP IN MINIMUM TEMPERATURE

If the air mass remains relatively constant for some days (in late autumn and early spring), the minimum temperature may be steady dropping, especially in the case of decreasing cloudiness (cooling by long-wave radiation).

Observed reactions. At first an avalanche of ducks, swans (and geese, at times late waders, occasionally passerine birds too) is likely to occur from inland waters to the coast. Later on, after some days, the movement will tend to slow down. The "head-to-wind attitude" is mostly observed in early morning and in the evening.

SUDDEN DROP IN MINIMUM VALUE AND CHANGE TO LARGE
DIURNAL AMPLITUDE OF TEMPERATURE

The frontal character is pronounced. Usually the air is much colder than the underlying ground or water surface. The wind direction is usually from the N

(—W). or N(—E). Not seldom there is also a rather strong wind and occasionally showers of cold rain or snow occur.

Observed reactions. On the cold mornings the birds are likely to be found in "head-to-wind" orientation, almost apathetic or asleep. Some birds may be killed by the cold. With rising temperature in the day, there will occur a migration S(W). It is "caused" by the chill but "released" by the rising temperature. It is of great interest that migration to the (N)E. will also occur during the sunny and warm part of the day at times, especially in the first months of the year.

Thus we find in the cases mentioned: (1) an apathetic "head-to-wind attitude" as the first response to the chill (and sudden change), (2) a southward migration, released in fact by the consequent warming by insolation, and (3) at times also an inland migration, released by the rise of temperature.

The significance of falling temperature is obvious, although the avian reaction to the change is not merely an uncomplicated flight from the cold area simultaneously with the drop in temperature. The releasing factor may be the subsequent warming and the direction of flight may be quite different at times.

(d) Fugitive reactions in birds on passing a front or a frontal zone between air masses

Most years in early spring some birds on vernal migration, birds such as *Corvus corone cornix*, *Alauda arvensis* (and *Vanellus*), on their migrations into and over Scania have to pass more or less pronounced limits between warmer air in the W. and colder air in the (N)E., at times rather local masses. In fact, there will also be found in the early morning a certain fugitive reaction to the cold masses, a tendency to a continuous return to the (warmer) coast. For some time in the morning the inward and outward movements seem to almost balance each other. Although the actual moment of turning is occasionally observed by the author, yet in many cases it will be difficult to prove that the observed behaviour is the response to low temperature. There are, however, cases of greater significance.

(e) Fugitive reactions to temperature inversions

Inversions near to zero. At times there has been in the morning a pronounced difference between a rather warm, local air mass over Öresund (the sound between Scania and Denmark) and the air over the coastal ice and the snow fields of western Scania, where nocturnal inversion has been generated over the ground.

Observed reaction. In a few instances the author has in such cases observed, how singing larks (*Alauda arvensis*) on vernal migration have ceased to sing and returned out over the water just at the moment of attempting to alight on the Scanian ground (MARKGREN in press). Here the fugitive element is obvious.

Inversions far below zero. The cases are in many ways outstanding, above all because of the physiological effect of wind and humidity that has been observed.
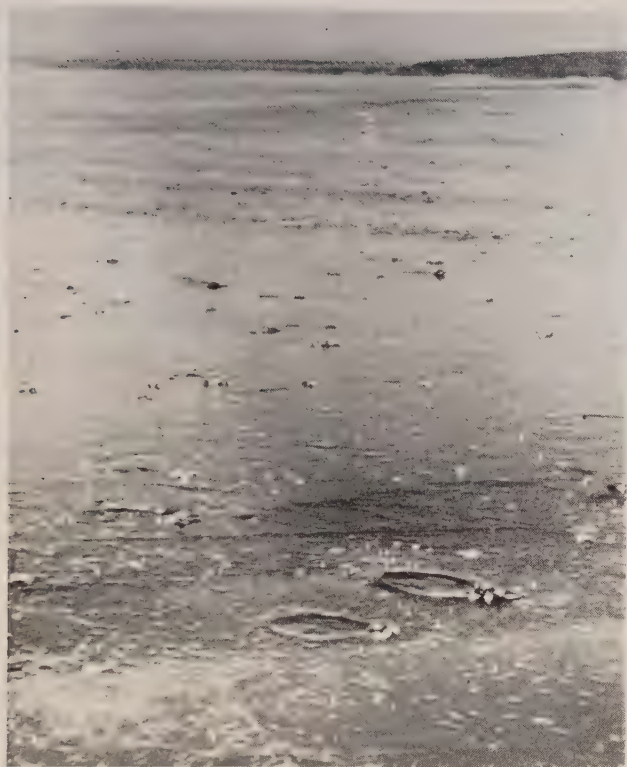
Parallelly arranged melting cavities and heaps of excrement on the ice are the typical traces left by geese facing the wind during their sleep. Here, the traces were left by a flock of *Anser fabalis* on the ice of Lake Sövdesjön. Photograph by G. MARKGREN, 4/2/59.

Here the wind effect, or rather the reaction to chilling effects of slight winds at low temperatures, should be mentioned in particular. Because of that complication, we will treat the matter under another heading.

(f) Reaction to "hidden" temperature factors

Reaction to chill of wind (and humidity) in low temperature conditions. In the case of severe cold and little horizontal wind in winter there is likely to occur at Sjölunda a nocturnal inversion over the surface of the ice. Cold air then flows down from higher parts of the locality, such as the quays, thus generating a slight gravity wind (a "catabatic" wind), the force of which may locally be greater than that of the great scale wind. In some cases, both winds join forces, especially in winds from the eastern quadrant. The relative humidity is usually high near the ice in the night and early morning. At times also a heavy radiation fog will occur. The avian reactions have been quite obvious.

The meteorological observations. The official records of temperature, wind and humidity registered at Lund and Malmö are used. Of course, the microclimatic

conditions over the ice have been at times much more accentuated than those of the official weather, especially as regards the humidity. Nevertheless, the main features of the weather situation have been quite obvious in the cases of special interest for the discussion, namely, the days with a temperature between $\pm 0°$ and $-18°C$ and a wind speed ranging from 0 to 2 (or seldom 4) m/sec. The real humidity value has, as mentioned, not been obtainable, and only an approximate figure and a general impression are given.

Observed reactions. Also when the wind speed is near to zero (m/sec) the birds, mostly gulls and ducks, are found to orientate themselves in the "head-to-wind attitude" (or "facing-wind attitude") against the "catabic wind" mentioned from the higher parts of the locality.

Interspecific differences of reaction. In *Larus* the sensitivity to chill by a slight wind at a low temperature is shown by the following order in the reactions in different cases: (1) *Larus canus* (most sensitive), (2) *L. ridibundus*, (3) (*L. marinus*), (4) *L. argentatus* (least sensitive). *L. marinus* is put in brackets, because the number of observed reactions is not of the same magnitude as that of the other species. For *L. canus* the temperature level seems to play a great part.

In *Anas* and *Anser* no interspecific differences are observed, as the observations in these special conditions are made up almost entirely of *Anas platyrhynchos* and *Anser fabalis*. Both these species, however, are found to react very sensitively with a "facing-wind" attitude and tending to sleep (cf. SWANBERG 1931, LÖWEGREN 1938).

In MARKGREN (1959) the author has presented a list of days with outstanding observations of "head-to-wind attitude" in birds, mostly gulls and ducks in the 12-year period from 1946 to 1957.

B. *Fugitive Reactions to Strong Wind*

(a) *Strong wind at temperatures below zero*

The conditions are more accentuated than in those with light winds. (Strong = more than 8 m/sec.)

Observed reactions. In these cases the gulls and ducks at the coast react about 100 % by "facing wind"; often they are also found asleep. Raptorial birds and passerines mostly take shelter in woods. These situations are sometimes fatal for the birds.

(b) *Strong winds at moderate temperatures*

Temperatures from $+0.5°$ to $9.5°C$ are noted as moderate.

Observed reactions. The behaviour noted in these situations does not differ from that observed in cases of higher temperature. Only one example will be mentioned

—the "facing wind" of thousands of *Aythya* on the lee side from land at Sjölunda (**MARKGREN** 1951 A). On *Charadriiformes*, see below.

(c) Strong winds at high temperatures

Temperatures above + 10°C (but usually below + 14°) are noted as high.

Observed reactions. The reactions in cases 2 and 3 are not distinguishable. Here observations were made on most Fennoscandian bird species. The bulk of observations is thus great.

Of most interest are the observations made on gulls, terns and waders on migration. They are found to react very sensitively to the wind by "head-to-wind attitude".

Briefly it can be said that any day at Sjölunda with a wind from the eastern quadrant with a speed of more than 12 m/sec during the period of vernal migration of terns, (gulls), waders and ducks, one can easily find a representative collection of the migrating species crowded tightly in a "facing-wind" position on the lee side of the vegetation, stones and so on. In just such cases the greatest flocks of *Sterna paradisaea* and *Chlidonias nigra* are to be noted at the locality.

On photographs of waders at the southern coast of England by E. HOSKING in SVÄRDSON & DURANGO 1950, p. 117, 118, 119, the birds are obviously facing wind, especially the oyster-catchers on p. 117. The behaviour of species typically adapted to a marine life on the open sea is not treated here.

Below are treated the observed reactions to precipitation. It must be mentioned immediately, however, that in most cases of heavy precipitation, there is also a strong wind and often a considerable drop in temperature too, if there are not very special conditions in a warm front. Notwithstanding this, there is a certain fugitive reaction to be found also in the case of minute winds during a snow fall. So we have to isolate the precipitation factor in our discussion.

C. Fugitive Reactions to Precipitation

(a) Light to heavy snow-fall and (strong) wind

This situation may occur in Scania any time between the end of October and the middle of April. In the mountains of Lapland it will occasionally occur in any month of the year. Consequently, the author has a mass of observations of avian fugitive behaviour in such weather conditions from any time of the year over a period of more than 20 years.

Observed reactions. In many ways the most outstanding are the fugitive reactions in reversed vernal migrations over Scania released as contemporary reactions to heavy snow-fall and wind. Certain instances of reversed migration are recorded in the literature (see above, Section I, D; cf. SVÄRDSON 1953). In MARKGREN (1960, Appendix) is presented a list of representative observations of reversed migrations in spring from 1948 to 1957. As is seen from these lists, the most out-

standing instances of reversed migration occur in response to heavy snow pre-
cipitation and wind, at times real snow-storms with an abundant precipitation.
In quite a number of cases the author has had the opportunity to follow the storm
situation and the consequent avian reactions to the slightest indications of events.

Summarizing, from the observations presented in the lists mentioned, the
following run of events is typical of the vernal situations in question:

Weather Situation Observed	Resting Birds	Reactions Observed in Migrating Birds
(1) Increasing wind but no precipitation. Turbulences.	Decreasing foraging activity.	Decreasing "normal" migration.
(2) Some snow and increasing wind.	"Head-to-wind" position of many birds.	Increase in number of resting birds.
(3) Heavy precipitation. Strong wind.	"Head-to-wind", common attitude, local movements for lee positions. Some birds breaking up.	Returning or alighting. Breaking up again.
(4) Snow-storm going on for hours without remarkable changes.	Increasing break-up for reversed migration. Induction is obvious.	Number of birds on reversed migration increasing in an incredible way. No "normal" migration.
(5) No changes.	Late in the evening apathetic birds may be found in shelter anywhere.	Decrease in number of birds in action.
(6) Change to "fine weather".	Increase in number of resting birds.	Both "normal" and reversed migration may occur.

The following features are outstanding:

(a) The resting birds cease their "normal" activity—foraging, sitting on the nest,
mating, playing, fighting or just preening their feathers.

(b) Resting or alighting birds take shelter in a typical "head-to-wind attitude".

(c) Birds on migration take shelter, as in (b) or mostly return in "reversed
migration".

(d) The number of birds on reversed migration over Sjölunda is often much
greater than that of birds on "normal" vernal or autumnal migration.

(e) During snow-storms with a visibility reduced to some tens of yards or less,
and regardless of wind direction, there occurs in western Scania under these
conditions a S. SW.-directed migratory movement in almost 100 % of birds
observed on the move. (This fact is of significance for the discussion of avian
power of orientation in migratory behaviour.)

(f) Resting birds at the initial moments of breaking up are obviously influenced
by birds already on the move (the induction effect).

(g) Since the air temperature has been mostly at, or below zero in the cases
mentioned, the chilling effect may have been of a certain significance in the be-
haviour.

(h) In spite of the possible temperature effect mentioned in the cases just treated, it is, however, quite obvious from the facts stated (1960, Appendix) that snow precipitation is a proximate factor in catastrophic avalanches of reversed vernal migration. It may be added that snow-storms are found to play just the same part in late avalanches of autumnal migrations (cf. the records of migration on the 23–26th of December, 1958, in Appendix, MARKGREN 1960).

In the following part of this chapter w shall find the fugitive behaviour more or less pronounced or as intention movements initiated by light to moderate snow-fall at a rather high temperature and in a light wind. Here the significance of the precipitation is obvious.

(b) *Light to moderate snow-fall and light wind at a temperature well above zero*

This situation is very common in Scania from the middle of March to the middle of May, at times also later on. In Lapland these weather conditions are likely to occur in the mountains also during the summer. Such a situation can be regarded as of little or no danger to the birds.

As a typical example are chosen the events at Lund on the 12th of April, 1957, (MARKGREN 1959 A). From 3.55 p.m. to 5.40 p.m. that day three light snow-falls occurred at a temperature changing between $-5°C$ and $+3°C$. In the showers there was a wind of some few m/sec.

Observed reactions. The reacting birds in a garden were 9 *Sturnus*, 20 *Passer*, and 3 *Columba palumbus*. In each case of snow-fall the birds ceased their foraging activity and were seen to take shelter in bushes in "head-to-wind attitude" or just "facing wind" *in situ*. Some of the birds moved about 100 yards before taking up the "facing-wind attitude". Between the showers the birds went on again with their foraging activities. The "head-to-wind attitude" was almost comical, as there was hardly any observable wind in this case.

It is of interest to compare this sensitivity to snow-falls with the behaviour observed on occasions with really hard wind but without any precipitation, when a certain crowding and "facing-wind attitude" has yet allowed a holding-territory activity. This sensitivity to snow-fall was observed on about 250 occasions.

Interpretation of the behaviour. Snow precipitation, with little or no wind seems to be a releaser of a fugitive behaviour, that is, the typical reaction to strong and/or chilling winds. This is probably the manifestation of an adaptation in surviving palaearctic bird species to frequent outbreaks of bad weather during their breeding period.

D. *Fugitive Reactions to the Weather Complex*

It has been mentioned above that there is a certain correlation between the winter and vernal weather situation as a whole and the run of migration in spring. Of course, both addictive and fugitive elements of behaviour can be deduced from the available observation series. That deduction, however, does not need

to be made here, for two reasons, (1) the bulk of observations of vernal migration demands a separate volume, (2) the problem in question has rather the character of indirect discussion, whereas the present paper is entirely based on direct observations.

3. On Fugitive-Behaviour Elements of Response to Disturbing Phenomena of Non-personal and Non-meteorological Environment

In the previous Section the use of the term "disturbance" was avoided, as it will be here in the following brief discussion. The reason for avoiding it in the present chapter is that the "disturbing" phenomena discussed here lack the character of direction in time, that is typical of personal disturbances and to some extent even certain meteorological phenomena. The "disturbances" treated below are characterized by a static extension in space. Nevertheless they are disturbing phenomena to be avoided (or escaped from) by the birds. Here only two outstanding phenomena will be discussed briefly.

A. *Ascent of Land-birds in Flight over Water*

In the course of normal migration in birds adapted to a life on the land, there is seen a certain tendency to vertical upward deviation, i.e. to a rising at the border of the sea or great lakes. RUDEBECK (1943) observed this behaviour in *Pica* and *Garrulus* and in crows, jackdaws and many species of passerine birds before the time of their main migration. At both Falsterbo and Sjölunda the present author has noted this behaviour in *Pica, Garrulus, Nycifraga, Parus, Prunella, Dendrocopus* (and *Dryocopus*) (cf. MARKGREN 1955). In birds that are poor flyers the rise is performed by intensified frequency of wing beats and changing the direction quite often but with a little positive vertical gradient, thus almost a caricature of the soaring behaviour. There are indications that the gradient of ascent in *Prunella modularis* may be dependent on visibility in the way of greater gradient at a better visibility. The following points are of importance here:

(1) A rising movement in front of water is seen in land-birds on migration.

(2) This behaviour, at times found in most species, is typical of poor flyers such as magpies.

(3) The significance of this behaviour is seen, when, for instance, magpies, thanks to height, are able to get back to the land after an unsuccessful attempt at migration.

(4) Obviously, this behaviour is caused by the sight of water in front of the migrating bird.

B. *Ascent and/or Deviation of Birds in Front of Towns*

A fugitive behaviour, somewhat related to the one just mentioned but very little known in fact, is the deviation and ascent observed at Sjölunda in passerine birds and *Vanellus* on reversed migration and in *Somateria mollissima* and in species

of *Branta* on normal vernal migration. Judging by that vertical and horizontal deviating behaviour, the city of Malmö acts as a real "Zugscheide" for the birds on reversed vernal migration or on an autumnal avalanche over that area. Four points have to be stressed:

(1) By means of the behaviour in question birds are found to avoid the town.

(2) The deviation and rise is not outstanding in passerine birds on reversed migration. It is found in all those species observed on catastrophic reversed migration in spring.

(3) This behaviour is also found in *Branta* and *Somateria* on vernal migration, especially on their taking course over Scania (cf. MARKGREN 1951).

(4) The fugitive moment is easily observable by the abruptness of deviation or ascent.

SUMMARY

The present paper on avian fugitive behaviour is based mainly on field study of wild birds in Fennoscandia and on simple experiments on birds in the field. The study was performed during a period of 16 years and in some cases over more than 25 years. Most observations were made at a coastal locality near Malmö in Scania. The first part of the paper (pp. 1–71) deals with avian reactions to disturbing phenomena ("disturbances") with a character of individuality and often with a spatial direction and a tendency towards momentaneousness. The second part (pp. 73–101) treats fugitive responses to disturbing qualities of the bird's environments, such as unfavourable weather changes.

Part I. "The disturbances" may be met by the bird with escape reactions or fighting. Some behaviour includes both reaction elements (mobbing behaviour, for instance). The following questions are discussed:

(1 *a*) On which disturbances do the respective bird species react?
(1 *b*) Which species react on the respective disturbances?
(2) How do the respective species react on the respective disturbances?
(3) How are the reactions arranged and organized as animal locomotor activity and as the performance of (geometrical) morphological patterns and as objective responses to physical influences?
(4) What are the biological significance and the origin of the reactions?
(5) What psychical experiences do these birds have?
(6) What are the releasing signals?

Chapter II treats of the concept of disturbance. The nature of different disturbing phenomena is described. These phenomena may be natural or artificial. Among the natural disturbances the raptorial birds are of most interest. The birds of prey are discussed here especially as regards their mode of hunting. Other kinds of natural biological and non-biological disturbances, such as artificial and experimentally arranged disturbances, are discussed. Here the concept of critical zones for hostile and fugitive behaviour is dealt with. These critical zones are different from species to species and may show intraspecific differences which are obviously dependent on the state of the birds and on the visibility and other weather elements. The bird's condition may also be influenced by meteorological elements.

Chapter III deals with possible fugitive and hostile reactions and their distribution in the species. The avian reaction to a potential danger will be to remain *in loco*, to take shelter, to take wing, to dive or else get away or resist the danger in some way. Remaining on the ground is a common behaviour in single birds, small flocks of passerines living on the ground, in some owls, some waders and many ducks and in *Rallus, Porzana, Crex* and some other species adapted to a life

close to the ground. The birds usually remain on ground that is not unfamiliar to the species as regards vegetation, texture or morphology. If the disturber is an avian predator and is moving fast and rectilinearly but not just in the direction of a sitting bird, then it is likely that this bird, regardless of species, will remain sitting on the ground. It may thus be a question of critical distance for (motional) reaction. An uncomplicated "escape *in situ*" as a simple reaction is, however, probably very rare. Alighting on the ground, in vegetation or other structures is a common way of escape in birds. Even alighting on water may at times be found in waders and more rarely in passerines. It is, however, a common misunderstanding that any bird tries to escape certain species of birds of prey by alighting and that it would remain safe having done so. Crowding in the air as an escape reaction is found typically in *Sturnus, Calidris* (and sometimes in *Plectrophenax*) when these birds are escaping the sparrow-hawk and the small falcons. It is seldom seen in *Anas* or *Aythya* as reaction to eagles or large falcons. Also in *Corvus* there may be found a sort of escape crowding. Crowding in the water is typical of *Aythya* and *Bucephala*. This behaviour was seen in *Mergus* except for *M. albellus*. Swimming escape, often with a considerable lowering of the value of the critical distance of escape reaction, is found in ducks and also in *Gaviiformes* and *Podicipitiformes*, in which a sort of "sink reaction" occurs as a fugitive reaction. The fast swimming escape, the running on the water and the running escape are discussed. Here also the taking-wing reaction is described and discussed as regards its relation to other fugitive reactions and its significance. The reaction to take wing for a disturbance is found in all the Fennoscandian birds studied from this point of view and in some species from southern and western Europe. This reaction will be seen as the answer to an approaching man, to avian or mammal predators or reptiles, to acoustic disturbances and to different artificial disturbances. It will be found as the spontaneous reaction to *Buteo, Aquila* or *Haliaeetus*, as well as to *Falco peregrinus*. The critical distance will show certain differences; the taking-wing reaction, however, will probably not be entirely lacking in any bird species as a reaction to animal disturbers at a certain critical distance, providing the bird has carrying wings. The important but difficult question of reduction and inhibition of escape is also treated in this connection. Finally mobbing and fighting behaviour are dealt with. The last part of Chapter III is devoted to a discussion of spatial patterns of commencing moments of fugitive motion. Here should be mentioned especially the circular flights of (mostly) ducks, when disturbed over small lakes or lanes in the ice, and the circuituous or elliptical motional curve by (mostly) gulls on eluding a danger. To the observer escape (and hunt) will often form a pattern, the structure of which is much dependent on outer ecological elements and, above all, on the birds involved. These geometrical patterns seem to be the results of complicated but balanced reactions by the escaping birds.

Chapter IV deals with interaction between the hunting predators and the hunted prey. First the predacious activity is described and the escape reactions observed are discussed. Then the delicate question of observable recognition of

predatory birds is treated. Much attention is bestowed on the fugitive error reactions. In birds there is found to be recognition of single persons (as mate and offspring) and of strangers and, finally, of predators. A great part of the surviving birds have to be reacting "too" sensitively and a considerable part of the other birds are likely to be caught in secondary reaction by induction. The more specialized the predation upon a bird species, the more exclusive is the reaction in the species found to be. And the more general (and frequent) the predation on the species, the more it will be found to show escape reactions to "harmless" phenomena, i.e. to non-specific disturbances. That is to say, the releasing signals are many in these birds. The escape-arousing properties of raptorial birds are treated. The most important ones seem to be shape, wing motion (and motion curve). Certain properties of hunt and escape flight are discussed. There are obvious specific differences in the flights. Yet from a physical point of view the possible patterns of hunting and escaping flight may be reduced to varieties of linear flight and deviation flight. The individual manner of the respective flights will be dependent on specific differences in anatomy, bulk of matter, habit and on the environments. Certain types of escape-flight behaviour are treated. The last part of this Chapter deals with the question of fear in captured escaping birds. First there is an attempt at interpretation of the scream of a captured bird. Then are discussed in order: the hypothetical fear in an attacked bird, the subjective fear in non-hunted birds and the escape *in vacuo*. Anthropomorphistic terms should be avoided.

Part II. In this part both fugitive and "addictive" behaviour are treated. Fugitive responses to environment changes and qualities, the fugitive reactions found in birds wintering and on migration are discussed. The first part of Chapter V deals entirely with definitions and classifications of wintering and migratory behaviour elements. Current bases of classification of the migratory behaviour complex are time of season, spatial extension and direction, the cyclic or non-cyclic characters, differences of internal motivation and sensitivity to external stimuli and the diurnal rhythm. Juvenile vagrancy is treated. The classification basis suggested by WILKINSON is also discussed here. The current use of the wintering concept is dealt with. Migratory movements in wintering birds and reversed migrations are discussed. Only some few "resident" bird species were found in Fennoscandia. Avian migration is suggested here as the (mostly) volant response, partly to spatial distribution of mainly food and shelter and partly to periodic environment changes caused by the planetarian rhythm, at times accentuated, or on the contrary, obscured by non-periodic modifications, which changes act as behaviour releasers (in a wide sense) in the bird, in which a corresponding (physiological) rhythm may be found.

Some aspects of "addictive" behaviour in migration are treated here in connection with a discussion of the guiding-line and the guiding-point effects. In, for instance, *Corvus, Garrulus, Buteo, Pernis, Numenius, Limosa, Larus* and *Stercorarius longicaudus* a certain addictive reaction to thermal and dynamic upwind currents is seen to cause a deviation of the migratory course. One chapter deals with the fugi-

tive-behaviour elements of response to weather in birds on wintering and migration. Among climatic and meteorological factors the temperature and especially its extreme values are likely to play a great part. But also the mean thermic conditions and what is found as avian response to them is treated here. Of a certain interest are also the hidden thermal effects in the humidity and the wind, which physical factors influence the physiological temperature, the "temperature experience" of the bird. In late October to December in Scania there is a steady drop in temperature even in the case of tropical maritime air invasions of long duration. Advection clouds and fog may restrict the cooling and limit the amplitude. A similar effect is obtained in tropical masses in winter high-pressure situations with light winds. The avian reaction is: (1) A slow migration from the inland towards the coastal localities, mostly observable as a contemporaneous change in number of birds, occasionally seen in actual movements. (2) A slow SW. migration away from the coasts. At times directly observed break-ups. (3) "Head-to-wind attitude" (Swedish: "motvindsattityd") and sleep during the coldest parts of the day. Often there are great crowds of birds tightly packed together in a sort of "escape *in situ*".

The behaviour is thus a slow adaptation with some fugitive quality. In the case of alternating fall and rise in temperature during the autumn an inland migration of birds was reported in the warmer periods. The observed avian reaction to a steady drop in minimum temperature, often with an influx of polar air, was first, a marked avalanche of ducks, swans, geese, passerines (and late waders at times) and later on, the "head-to-wind attitude" in the early mornings and in the evenings. On the other hand, a sudden drop in minimum value and a change to a large diurnal amplitude of the temperature caused: (1) an apathetic "head-to-wind" response to the sudden change, (2) a southward migration released in fact by the consequent warming by insolation, and (3) at times also an inland migration released by the rise of temperature.

Fugitive reactions to pronounced spatial changes of temperature were seen mainly in *Corvus*, *Alauda* and *Vanellus* when passing a front or a frontal zone between air masses on their vernal migration. Similar behaviour was demonstrated by *Alauda* in the early mornings as a reaction to (nocturnal) ground inversions over the coastal ice and the snow-fields of western Scania. Interspecific differences of reactions to cold wind (and humidity) in low-temperature conditions were found, for instance, in *Larus*. Outstanding fugitive reactions to snow precipitation were noted during the vernal migration in many bird species such as *Sturnus*, *Turdus*, *Fringilla*, *Vanellus*, *Numenius*, *Charadrius* and *Haematopus*. In snow-storms these birds and some other species demonstrated decided reversed migrations often on a large scale as regards number and intensity. The course was south to south-west, regardless of direction of wind, which is of interest for the discussion of avian orientation in weather situations with very bad visibility and without sun (MARKGREN in press). The number of birds on reversed migration over Sjölunda is often much greater than that of birds on "normal" vernal or

autumnal migration. The induction effect is often quite obvious at the initial moments of breaking up. In spite of possible temperature effects in these cases, it is obvious that snow precipitation is a proximate factor for catastrophic avalanches of reversed vernal migration. Snow-storms are also found to play the same part in late avalanches of autumnal migrations. Reactions to light-to-moderate snow-fall and light winds at temperatures above zero are treated. The last few pages deal with behaviour elements of response to disturbing phenomena of non-personal and non-meteorological environment. Two outstanding phenomena are discussed, namely, the ascent of land-birds on flight over water and ascent and/or deviation of birds in front of towns.

Thus, in the discussion of avian fugitive reactions the author has gone from well-defined and easily observable escape reactions to more complicated fugitive behaviour, at times involved in other sorts of activity. This disposition of the matter has been used to demonstrate that most fugitive behaviour is composed of many single reactions and may often overlap with different kinds of behaviour. Fugitive behaviour may, like any other sort of behaviour, be treated from ethological, ecological or genetic aspects. Genetic questions are, however, almost entirely avoided here.

Certain definitions of ethological and ecological concepts are discussed. These definitions are intended only as arbitrary ones in order to facilitate the discussion.

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APPENDIX I

LIST OF
ABBREVIATIONS AND SYMBOLS

The Behaviour of the Predatory Birds

S = sitting.   F   = flying.
T = taking wing.   O   = flying over.
Sl = descending and settling.   H   = hunting.
f = fishing (*Haliaeetus, Pandion*).   (H) = hunting in a successful hunt

Reactions of the Hunted or Disturbed Birds

(+) = alarm and/or intention   + m   = escape reaction proceed-
        movements.   ing into migration.
 +   = (alarm and) rising.   + mW = escape reaction proceed-
M   = mobbing.   ing into migration west-
 + S = reaction of a short dura-   ward.
        tion.   + mE = escape reaction proceed-
R   = "flying round", circular   ing into migration east-
        flight.   ward.

Captured prey in a successful hunt is mentioned in brackets ().
The number of reacting birds has been counted only in the minor bird
flocks, otherwise estimated.

Initials of Persons (Observers) Mentioned in the Comments

S. A.   = Sune Andersson   Hj. M.   = Hjalmar Mattsson
B. B.   = Bo Bergstedt   O. M.   = Olof Mohlin
G. B.   = Gustaf Borgström   L. O.   = Lennart Otterhag
L. B.   = Lars Broberg   G. O.   = Gunnar Otterlind
B. C.   = Bertil Carlberg   G. R.   = Gustaf Rudebeck
E. D.   = Erik Dahl   L. R.   = Louis Rydbeck
A. E.   = Anders Enemar   A. S.   = Allan Strandsjö
B. F.   = Bengt Fritz   E. Sv.   = Erland Svennilson
E. H.   = Erik Hansen   L. S.   = Lars Svensson
T. H.   = Torsten Herner   N. T-W.   = Nils Tarras-
B. H-C. = Björn Hyltén-   Wahlberg
          Cavallius   S. U.   = Staffan Ulfstrand
T. M.   = Torsten Malmberg   K. G. W. = Karl Georg
G. M.   = Gunnar Markgren   Wingstrand
M. M.   = Martin Markgren

DISTURBANCES AND OBSERVED REACTIONS
OF THE BIRD FLOCKS IN TABULAR
FORM BY SPECIES

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		ASIO FLAMMEUS				
I	S, F, S	*Larus argentatus*	—	25/2/47	Sjölunda	
		Corvus corone cornix	+ M	25/2/47	Sjölunda	
I	O	*Corvus corone cornix*	+	16/2/47	Lund, W.	
I	O	*Pica pica*	+ M	28/5/47	Nymö mosse	
I	O	*Corvus corone cornix*	M	29/5/47	Nymö mosse	
		Larus ridibundus				
I	Sl	*Vanellus vanellus*	(+)	1/11/49	Krankesjön	
I	O	1 *Corvus corone cornix*	+ M	5/2/50	Sjölunda	A.E. & M.M.
I	F	1 *Larus argentatus*	+ M	16/3/50	Sjölunda	A.E. & M.M.
I	F	*Larus*	—	7/4/50	Sjölunda	
I	F	*Larus*	+ M	23/3/52	Sjölunda	
13	F	*Larus argentatus*	+ S	4/1/53	Sjölunda	
		Corvus corone cornix	+ M			
2	F	*Larus ridibundus*	+ S	17/3/53	Lomma	
16	F	*Larus* (flocks)	(+)	26/12/53	Sjölunda	G.B.
I	T	*Larus* (flocks)	(+)	30/12/53	Sjölunda	
6	T	*Larus argentatus*	+ S	3/1/54	Sjölunda	G.M. & M.M.
3	F	*Larus argentatus*	(+)	24/1/54	Sjölunda	G.B. & M.M.
		Corvus corone cornix	M			
I	F	*Corvus corone cornix*	M	10/1/55	Sjölunda	
I	F	*Corvus monedula*	(+)	2/1/56	Lund, W	Seen 2/1 −9/3.
2	F	*Corvus*	(+)	27/1/56	Sjölunda	
3	F	20 *Corvus corone cornix*	+ S	3/2/57		
		100 *Larus argentatus*	+ S	3/2/57	Sjölunda	
		5 *Larus argentatus*	+ M		Sjölunda	
2	F	40 *Larus argentatus*	+ S	10/3/57	Sjölunda	
		2 *Larus argentatus*	M			
		ASIO OTUS				
10	S, F, S	*Pica pica*	(+)	2/3/47	A churchyard at Lund.	Dec.– Feb.
		Parus sp.	(+)			
5	S, F, S	*Pica pica*	M	17/1/48	A churchyard at Lund.	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	S	*Pica pica*	—	15/2/48	A churchyard at Lund.	
1	O	6 *Anthus*	—	6/10/49	Falsterbo	
1	F, Sl	8 *Larus argentatus*	+ M	6/10/49	Falsterbo	
1	H	Passerine birds	+ S	7/1/51	Sjölunda	
1	F	*Chloris chloris*	+ S	4/1/53	Sjölunda	

FALCO RUSTICOLUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1 juv.	F	*Larus argentatus*		9/1/49	Sjölunda	G.R.
	O	*Larus argentatus*				
1 juv.	H	*Larus argentatus*	+	22/1/49	Sjölunda	S.A., A.E. & M.M.
1 juv.	F, Sl	*Anas platyrhynchos*		27/2/49	Sjölunda	S.O.F. exc.
		Anas crecca (150)	+ S			
		Vanellus, Larus	+ S			
1 juv.	H	*Larus ridibundus*				
		Larus canus	+ R	5/3/49	Sjölunda	B.H-C. & M.M.
		Larus argentatus				
1 juv.	O	*Columba* (flock)	—	5/10/50	Falsterbo	On migration.
1 juv.	H	*Anas + Larus*	+	1/1/51	Sjölunda	Hj. M.
1 juv.	F. Sl	*Larus argentatus*	+	2/1/51	Sjölunda	
		Anas platyrhynchos				
1 juv.	H	*Anas + Larus*	+	2/1/51	Sjölunda	Hunted only *Larus ridibundus.*
		Corvus corone cornix				
		1 *Larus argentatus*	M			
1 juv.	H	*Corvus corone cornix* (1 + 1 + 100)	+	6/1/51	Sjölunda	Hunted single crows and flocks.
1 juv.	H	*Corvus, Larus*	+	19/1/51	Sjölunda	
		Corvus frugilegus				
1 juv.	H	*Larus ridibundus*	+	25/1/51	Lund N.	
		Larus canus				
		Larus argentatus				
		Larus argentatus				
1 juv.	H	1 *Corvus corone cornix*	+	23/2/51	Sjölunda	Hunted gulls.
		60 *Vanellus vanellus*	+			S.A. & M.M.
1	H	2000 *Vanellus vanellus*	+	28/11/51	Sjölunda	
		1000 *Vanellus vanellus*	+			
		400 *Charadrius apricarius*	+			

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		Charadrius	+			
		Corvus corone cornix	+ S			
		Larus ridibundus	+			
1	H	17 *Tadorna tadorna* ⎫ 3500 *Anas platyrhynchos* ⎭	+ R	25/12/54	Sjölunda	
		20 *Anas crecca*				
		2000 *Aythya, Bucephala* ⎫ *Somateria* ⎭	+ S			
		2 *Mergus merganser* ⎫ 9 *Mergus albellus* ⎭	+			
		Larus (flocks)	+ R			
1	O	1 *Buteo buteo*	—	30/3/56	Holmeja	G.M. & M.M.
2	O	*Rissa, Alcae*	+	18/8/56	Veddöy Röst (Norway)	G.M. & M.M.
		Larus argentatus				
1	F	*Larus ridibundus*	—	21/3/57	Krankesjön	S.U.

FALCO PEREGRINUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
2	O	2 *Corvus corvus*	+ M	14/7/47	Lilla Karlsö	Gotland
		Larus argentatus				
		Larus fuscus				
1	O	*Sterna* spec.	+ S	16/7/47	Lina Myr	Gotland
		Chlidonias niger				
1	M	*Pandion haliaëtus*	S + S	10/8/47	Löddeå	
	F	2 *Accipiter*	M	10/8/47	Löddeå	
1	H	200 *Vanellus vanellus*	+	24/8/47	Krankesjön	
		2 *Tringa*				
1	H	*Corvus corone cornix*	+	26/8/47	Lomma	
		Larus argentatus	+	26/8/47	Lomma	
		20 *Tringa nebularia*	(+)	26/8/47	Lomma	
1 ad.	F	*Vanellus + Tringa*	+ S	26/8/47	Löddeå	
	Sl	3 *Pandion haliaëtus*	1 + M	26/8/47	Löddeå	
2	H	*Larus argentatus*	(+)	16/9/47	Mölle	
1	H	*Columba oenas*	+	14/9/49	Falsterbo	The dove lagging behind in a flock.
1 juv.	H, Sl	*Pica pica*				
		Falco tinnunculus	+	22/9/49	Falsterbo	The falcon gave up and settled.
1	H	*Columba palumbus* (400)	+	4/10/49	Falsterbo	
		1 *Columba palumbus*				15 swoops, no success.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	1 *Garrulus glandarius*	+	6/10/49	Falsterbo	
		1 *Aulada arvensis*	+			
		1 *Fringilla*	+			
		20 *Columba oenas*	+			
		Larus (*argentatus*)	+			
1	H	2 *Turdus viscovorus*	+	6/10/49	Falsterbo	
		Carduelis ? (flock)	+			
1	H	1 *Columba palumbus*	+	9/10/49	Falsterbo	2 light
1 ad.	O(H)	7 *Corvus corone cornix*	+	10/10/49	Falsterbo	swoops.
	M	1 *Larus marinus*				
1	H	*Columba* (flock)	+	11/10/49	Falsterbo	16 swoops.
	F	*Columba* (flock)	—			The doves on migration.
1	S	2 *Accipiter nisus*	M	16/12/49	Havgård, p.106	S. A., A.E. & M.M.
1	O	(100) *Fringilla*	—	19/2/50	Börringe	S. A., A.E. & M.M.
		Emberiza citrinella				
		Alauda				
1	H	*Larus ridibundus*	+R	3/4/50	Sjölunda	
		Larus canus				
		Larus argentatus				
1	H	20 *Vanellus vanellus*	+m	7/4/50	Sjölunda	
1	H	Small birds	+	1/10/50	Falsterbo	On migration.
1	H	*Columba*		3/10/50	Falsterbo	3 swoops
1	H	Passerine birds	+	5/10/50	Falsterbo	6 swoops.
1	H	*Anthus pratensis*	+S	5/10/50	Falsterbo	
1	H	*Corvus monedula*	+	10/1/51	Trolleberg	O.M. & M.M.
		Columba livia				
1	H	*Columba*	+	11/1/51	Trolleberg	O. M.
1	H	1 *Turdus pilaris*	+S	31/1/51	Sjölunda	20 swoops.
		1 *Larus ridibundis, canus, argentatus*	+S			
		2 *Corvus corone cornix*	+			
		1 *Fringilla*	+S			
		Corvus corone cornix (flock)				
	M	1 *Ardea cinerea*	(F)			
		1 *Haliaeetus albicilla*	(F)			
1	H	*Corvus corone cornix*	+	3/2/51	Sjölunda	Hunting badly. A.E.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Corvus corone cornix* *Larus ridibundus, canus* *Larus argentatus*	+ S	9/2/51	Sjölunda	The falcon hurt in its right wing.
1 juv.	(H)	*Larus* (*Larus ridibundus*)	+ R	11/2/51	Sjölunda	Horizontal hunt.
1 juv.	H	*Larus*	+ R	14/2/51	Sjölunda	The hurt falcon.
1 juv.	H	*Larus* 6 *Alauda arvensis*	+ + S	18/2/51	Sjölunda	The hurt falcon.
1	H	*Corvus corone cornix* *Sturnus vulgaris*	+	11/3/51	Sjölunda	
1	H	*Corvus corone cornix* (250) *Larus* (7000)	+	15/3/51	Sjölunda	
1	T, M	*Buteo lagopus*	O	17/3/51	Sjölunda	
3	H	*Larus* *Anas, Aythya* *Corvus corone cornix* *Turdus viscivorus* *Turdus pilarus*	+ R + + +	18/3/51	Sjölunda	1 falcon, the hurt one. S.O.F. exc. A.E., T.M., Hj.M. & M.M.
1	H	*Anas, Tadorna* *Larus, Calidris* *Sterna*	+ R + S + S	21/4/51	Sjölunda	
1	H	*Larus ridibundus* *Larus canus* *Larus argentatus* *Larus argentatus* *Larus argentatus* (flock)	+ + R M +	12/5/51	Sjölunda	
1	H	3000 *Vanellus vanellus* *Anas*	+ (—+m)	23/9/51	Sjölunda	
1 juv.	H	200 *Larus ridibundus* 1 *Corvus corone cornix* 2 *Larus argentatus* 1 *Falco tinnunculus* 5000 *Vanellus vanellus*	+ + + + + S	23/9/51	Sjölunda	1 attack. 4 attacks. Hunted as a merlin.
1	H	8000 *Vanellus vanellus* 4500 *Larus ridibundus* 200 *Charadrius apricarius* 500 *Calris alpina* 8 *Tringa totanus* 700 *Anas* (*platyrhynchos, penelope*)	+ + + + + S + R	10/11/51	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		Anas crecca	+ R, Sl.			
		100 *Larus argentatus*	—, +			
		8 *Larus argentatus*	M			
		The falcon hunted all these species, not the rising flocks but single birds outside the flocks. *Anas crecca* down on to the water. The hunt lasted 15–20 min.				
1	H	*Larus ridibundus*	+			
		Larus argentatus	+ R	11/11/51	Sjölunda	
		12 *Larus marinus*	—			Note *L. marinus*
		1 *Larus marinus*	M			
		Charadrius apricarius	+			
		Vanellus vanellus	+			
		Anas platyrhynchos, penelope	+ R			
		100 *Anas crecca*	+ R			
		10 *Anas crecca*	+ Sl			Note *A. crecca*
1	H	*Anas, Larus, Corvus*	+	16/12/51	Löddeköpinge	
1	H	*Larus argentatus*	+	8/1/52	Sjölunda	
		Larus ridibundus	+ R			
		50 *Corvus corone cornix*	+ M			30 swoops
		Anas crecca	+ R			
1	(H)	(1 *Anas crecca*)		7/5/52	Sjölunda	1 swoop
	Sl	*Larus, Vanellus*	+ M			
		Haematopus				
1	O	50 *Larus ridibundus*	÷	14/5/52	Furunäsviken (Skellefteå)	G.M. & M.M.
		2 *Numenius arquata*				
1	H	1800 *Larus ridibundus*				
		20 *Larus canus*				
		5000 *Larus argentatus*	+ R	16/12/52	Sjölunda	No swoops
		100 *Larus marinus*				
		2000 *Anas platyrhynchos*	÷			
		Corvus	÷			
1	H	*Corvus corone cornix*				
		Corvus monedula	+	21/12/52	Sjölunda	
		Larus				
1	H	200 *Corvus corone cornix*				
		Larus (flocks)	+	4/1/53	Sjölunda	
		Turdus pilaris (flock)				
		4 *Columba palumbus*	÷			
1	O	10 *Chlidonias* (flock)	(+)	21/5/53	Sjölunda	
		Sterna				
2	H	*Limosa lapponica*				G.M. & M.M.
		Numenius arquata	÷	29/8/53	Sjölunda	
		Tringa, Calidris				

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Tringa, Calidris*	+	30/8/53	Sjölunda	G.M. & M.M.
5	O	*Anas, Larus*	+ S	1/9/53	Löddeå	G.M. & M.M.
2	H	*Corvus, Larus, Anas* ⎫	+			L. Svens-
1	(H)	*(Anas platyrhynchos)* ⎭		21/3/54	Sjölunda	son &
		Anas, Larus	+ R			M.M.
	S	370 *Corvus corone cornix*	M, Sl			
	T	*Corvus corone cornix*	+			
1	F	*Corvus, Larus* ⎫	+	25/3/54	Sjölunda	G.M. &
		Anas, Vanellus ⎭				M.M.
1	O	*Bucephala*	—	21/8/54	Luleluspen (Lappland)	G.M. & M.M.
1	H	*Anas* (flock)	+	6/11/54	Foteviken	S.U., T.H., M.M. *et al.*
1	H	*Larus ridibundus* ⎫	+	21/11/54	Lomma	
		Larus Canus/argentatus ⎬				
		Corvus ⎭				
1 ♂	H	*Anas, Corvus*	+			
		Larus (flocks)	+ R	8/1/55	Sjölunda	

First the gulls radiated out from the falcon, settling with its prey.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1 ♀	(H)	*Anas, Aythya* (flocks)	+ R	8/1/55	Sjölunda	
		(Mergus albellus)				
	Sl, S	100 *Corvus corone cornix*	M			
		250 *Larus argentatus*	+ R–M			
	H	*Corvus corone cornix* ⎫	+			
		Larus, Anas, Aythya ⎭				

The falcon had to leave the smew for the gulls, then it started hunting crows.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Corvus corone cornix*	+			
		Anas, Aythya	+ R	20/1/55	Sjölunda	
		Larus				
1	O	10 *Corvus corone cornix*	(+)	21/1/55	Sjölunda.	Radia-
		1000 *Corvus corone cornix*	(—)			tion fog.
		16,000 *Larus*	—(+)			
		12,000 *Aythya, Bucephala*	—			
		5000 *Anas*	—			
		Mergus				
1	O	*Corvus, Larus* (flocks)	+ R	2/2/55	Sjölunda	
3	H	17,000 *Larus*	+ R	5/2/55	Sjölunda	
		Corvus	+			
1 juv.	H	*Corvus corone cornix*	+			

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		Larus (flocks) ⎱ *Anas, Aythya* ⎰	+ R			
1 juv.	H	*Anas, Aythya* ⎱ *Mergus abellus* ⎰	+ R	23/2/55	Sjölunda	The bill of the
		Larus (flocks)	+ R			falcon probably injured.
	(H)	(*Anas platyrhynchos*)				
	S	*Larus argentatus* ⎱ *Corvus corone cornix* ⎰	M			The falcon had to let the
		(*Anas platyrhynchos*)	+, Sl			mallard fly back to its hole in the ice. S.A., A.E. & M.M.
1	H	*Fringilla, Cloris*	+ S	25/2/55	Sjölunda	
		500 *Corvus corone cornix*	+ S			
		10,000 *Larus ridibundus + arg.*	+ R			
		7000 *Anas platyrhynchos*	+ S			
1	H	6000 *Larus*	+, + mE	20/3/55		
		Corvus corone cornix	+			
		Corvus monedula	+ mE			
1	S	*Larus*	—	27/3/55	Sjölunda	
1	(H)	1 (*Larus ridibundus*)		28/3/56	Sjölunda	
		> 10,000 *Larus*	+			
		2000 *Anas platyrhynchos*	+			
		45 *Haematopus*	+			
		Calidris				
1	H	5–7000 *Larus argentatus*	+ R			
		97 *Numenius arquata*	+ mE, W	25/4/56	Sjölunda	
		Vanellus (flock)	+ m			
		Calidris (flock)	+ (R)			
1	O	5–6 *Columba palumbus*	(S)—	7/10/56	Havgård, p. 106	
1	H	*Anas, Aythya* (flock)	+ S	25/12/56	Hammarsjön	
1	H	*Aythya, Mergus*	—	6/2/57	Häckeberga	B.C. & M.M.
		20 *Anas platyrhynchos*	+ R			
1	O	200 *Anser fabalis*	+ R			
		Aythya, Mergus	+			
1 ad.	H	*Larus* (flocks)	+	11/4/57	Sjölunda	
		30 *Calidris alpina*	+			
		4 *Corvus, Monedula*	⋮			
		2 *Corvus frugilegus*	+			
		74 *Numenius, arquata*	—			
		1 *Recurvirostra*	—			

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		1 *Charadrius*	—			
1	H	*Larus ridibundus*	+	29/4/57	Sjölunda	
		Larus argentatus	+			
		Vanellus	+			
		Calidris	+			

FALCO COLUMBARIUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Larus ridibundus*	(+)	16/8/47	Snogeholmssjön	
1	H	*Calidris alpina*	+	7/11/48	Sjölunda	
		Vanellus vanellus	+			
1 ♂	H	*Larus ridibundus*	(+)	5/5/49	Krankesjön	B.H-C. & M.M.
1	H	*Troglodytes troglodytes*	+	13/9/49	Falsterbo	
1	H	*Anthus pratensis*	+S	14/9/49	Falsterbo	
		Motacilla alba + flava	+S			
		Carduelis spinus	+S			
1	H	*Carduelis?*	+	15/9/49	Falsterbo	
1	H	*Carduelis spinus*	+	16/9/49	Falsterbo	
1	H	*Carduelis spinus*	+	16/9/49	Falsterbo	
1	H	*Carduelis spinus*	+	16/9/49	Falsterbo	
2	H	1 *Carduelis spinus*	+	16/9/49	Falsterbo	2 *Falco colum-barius* + 1 *Accipiter nisus.*
1	H	*Carduelis spinus*	+	16/9/49	Falsterbo	
1	(H)	(*Carduelis spinus*)	+	17/9/49	Falsterbo	*Falco* on migra-tion.
1	H	*Sterna sandvicensis*	+	21/9/49	Falsterbo	
1	H	Small bird	+	24/9/49	Falsterbo	
1	H	Small bird	+	25/9/49	Falsterbo	12 swoops.
1	M/H	*Corvus corone cornix*	+	26/9/49	Falsterbo	4 swoops.
1	H	*Carduelis spinus*	+	27/9/49	Falsterbo	
1	H	2 *Larus argentatus*	+M	28/9/49	Falsterbo	
1	H	*Columba*	+	28/9/49	Falsterbo	G.R.
1	H	45 *Fringilla coelebs*	+	28/9/49	Falsterbo	"Thrush flight"
1	H	1 *Anthus cervinus*	+	28/9/49	Falsterbo	
1	(H)	(*Carduelis spinus*)	+	2/10/49	Falsterbo	
1	H	*Calidris* (flock)	+	4/10/49	Falsterbo	
1	H	100 *Carduelis spinus*	+	5/10/49	Falsterbo	Hunted in the flock.
1	H	*Carduelis spinus*	+	5/10/49	Falsterbo	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
I	H	*Regulus regulus*	+	9/10/49	Falsterbo	3 swoops.
I	H	*Larus ridibundus*	+	11/10/49	Falsterbo	
I	H	*Anthus*	+	30/9/50	Falsterbo	7 swoops.
I	(H)	(*Carduelis*)?		30/9/50	Falsterbo	
I	H	*Fringilla montifringilla*	+	30/9/50	Falsterbo	
I + I	H	*Anthus pratensis*	+	1/10/50	Falsterbo	
I	H	14 small birds	+	1/10/50	Falsterbo	
		1 *Fringilla coelobs*	+ S			The merlin made 7 swoops, then hovered over the rose bush, where the finch escaped. Then 38 swoops.
I	H	*Hirundo rustica*	+	1/10/50	Falsterbo	
I	H	*Carduelis*	+	2/10/50	Falsterbo	
I	(H)	(*Fringilla coelebs*)/flock	+	2/10/50	Falsterbo	8 swoops. One finch lagging behind was captured.
2	H	*Fringilla coelebs*/flock	+	3/10/50	Falsterbo	
I	H	*Anthus pratensis*	+ S	5/10/50	Falsterbo	2 swoops.
I.	H	*Fringilla*	+	5/10/50	Falsterbo	
2	H	*Fringilla coelebs*	+	5/10/50	Falsterbo	7 + 4 swoops.
I	H	*Anthus pratensis*	+ S	5/10/50	Falsterbo	Seized over the sea.
I	(H)	(Passerine bird)		5/10/50	Falsterbo	
I	H	*Anthus pratensis*	+ S	5/10/50	Falsterbo	1 swoop.
I	(H)	(Passerine bird)	+	5/10/50	Falsterbo	
I	H	*Anthus*	+ S	5/10/50	Falsterbo	
I	H	*Nucifraga caryocatactes macro-rhynchos*	Sl	5/10/50	Falsterbo	The *Nucifraga* made a

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
						swoop into a garden, thus escaping.
1	H	Small bird	+S	5/10/50	Falsterbo	The small bird escaped into a bush.
2	H	*Anthus pratensis*	+S	6/10/50	Falsterbo	
1	H	200 *Fringilla coelebs*	+	6/10/50	Falsterbo	The finches, on migration, escaped into a garden.
1	H	*Anthus pratensis*	+	6/10/50	Falsterbo	
1	H	*Alauda arvensis*	+	2/1/50	Sjölunda	3 attacks.
1	H	*Anthus pratensis* *Plectrophenax nivalis*	+	24/1/51	Sjölunda	
1	H	*Calidris, Tringa, Charadrius, Haematopus*	+	1/4/51	Saxån	
1	H	50 *Calidris alpina* 24 *Fulica atra*	+m +m	26/4/51	Sjölunda	
1	H	*Tringa + Charadrius*	+	11/8/51	Karesuando	(Lappland)
1	H	*Motacilla*	+S	12/9/51	Falsterbo	
2	H	*Anthus*	+	15/9/51	Falsterbo	
1	H	*Anthus ?*	+S	16/9/51	Falsterbo	
2	H	*Anthus, Calidris*	+S	23/9/51	Sjölunda	
1	H	80 *Carduelis*	+S	30/12/51	Sjölunda	The merlin did not hunt into the flock.
1	H	*Carduelis flavirostris*	+S	8/1/52	Sjölunda	
1	H	*Carduelis, Fringilla*	+S	19/1/52	Sjölunda	
1	(H)	(*Aves ? Mammalia ?*) *Carduelis*	X +S	10/2/52		
1	H	*Alauda arvensis*	+	27/2/52	Sjölunda	
1	H	*Motacilla*	+	26/4/52	Sjölunda	
2	H	*Hirundo rustica* *Philomachus* (flocks) *Tringa* (flocks)	+ —	18/5/52	Furunäsviken (Skellefteå)	G.M. & M.M.
1	H	*Hirundo, Anthus*	+	11/10/52	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
I	(H)	(*Regulus regulus*)		21/9/53	Falsterbo	
I	H	*Parus* (flocks)	+S	21/9/53	Falsterbo	
I	H	*Alauda arvensis* *Corvus monedula*	+	8/11/53	Sjölunda	
I	H	*Fringilla, Carduelis* *Emberiza schoeniclus*	+	15/11/53	Sjölunda	G.M.
I	H	3 *Sturnus* *Motacilla, Anthus*	+	4/5/54	Sjölunda	
I	H	*Corvus monedula*	+	6/2/55	Lund	
		Turdus merula	+	6/2/55	Lund	
I	H	*Fringilla chloris*	+S	11/2/55	Sjölunda	
		30 *Corvus monedula* 4 *Corvus frugilegus* 2 *Corvus corone cornix*	+S +			
		300 *Corvus corone cornix*	+ mE			
I	H	2000 *Fringilla, Chloris* *Carduelis flavirostris*	+S	22/2/55	Sjölunda	
		100 *Larus argentatus* *Corvus corone cornix*	+S			
		Corvus corone cornix	+ M			
I	H	*Fringilla, Chloris* *Carduelis, Emberiza*	+S	23/2/55	Sjölunda	S.A., A.E. &
		500 *Larus argentatus*	+S			M.M.
		100 *Corvus*	+			
I	H	50 *Fringilla, Chloris*	+S	24/2/55	Sjölunda	
		Corvus (flocks)	+S			
		800 *Larus argentatus* 200 *Larus ridibundus*	+S			
I	H	100 *Fringilla, Chloris*	+S	25/2/55	Sjölunda	
		300 *Corvus*	(+)			
		1000 *Larus*	+			
I	H	*Carduelis*	+S	5/3/55	Sjölunda	
		Corvus, Larus	+			
I	H	*Carduelis*	+S	8/3/55	Sjölunda	
		Corvus, Larus	+S			
I	H	*Turdus, Alauda*	+S	23/10/56	Benestad	
I	H	*Turdus, Bombycilla*	+S	17/2/57	Bonderup	
I	H	*Larus ridibundus* (flocks)	+S	29/3/57	N. Degerhamn	"Thrush
		Vanellus (scattered)	+		(Öland)	flight".
		Charadrius	+			

FALCO TINNUNCULUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
I	H	*Chloris, Passer montanus*	+S	21/3/48	Sjölunda	
		Fringilla, Motacilla alba	+S	21/3/48	Sjölunda	
		Vanellus vanellus	—			
I	H	*Carduelis spinus*	+	25/9/49	Falsterbo	4 swoops.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Pica pica*	M	5/10/49	Falsterbo	
1	H	15 *Anthus pratensis*	+	5/10/50	Falsterbo	The kest-
		1 *Anthus pratensis*	+			rel hun-
		1 *Emberiza schoeniclus*	1)—			ted just
			2) +			behind a
						sparrow-
						hawk.
1	O	*Calidris*	+ S	19/4/50	Sjölunda	
1	(H)	(*Passerine birds*)	+ S	14/5/50	Sjölunda	
1	H	*Columba livia* (25)	+	10/1/50	Trolleberg	
1	H	*Anthus* ?	+	27/3/51	Sjölunda	
		Sturnus vulgaris				S.A.,
1	H	*Anas crecca*	+	6/4/51	Sjölunda	O.M. &
		(90) *Limosa lapponica*				M.M.
1	(H)	*Motacilla alba*	+ S	12/9/51	Falsterbo	
2	H	*Anthus*	+ S	23/9/51	Sjölunda	
1	O	*Charadrius*	+ S	2/9/52	Sjölunda	
		Calidris				
1	O	*Corvus monedula*	+ S	4/1/53	Sjölunda	
	H	*Emberiza schoeniclus*				
1	H	*Carduelis, Chloris*	+	8/11/53	Sjölunda	
		Anthus	—			
1	H	*Alauda, Parus*	+	1/1/55	Sjölunda	
1	H	*Alauda, Turdus*	+ S	2/1/55	Sjölunda	
1 ♀	H	*Carduelis*	+	5/1/55	Sjölunda	
		Turdus	+ S			
1	H	*Carduelis, Fringilla*	+ S	8/1/55	Sjölunda	
1 ♂	H	30 *Fringilla*	+ S	24/1/55	Sjölunda	
		10 *Emberiza citrinella*				
		5 *Corvus frugilegus*	+			
		1 *Corvus corone cornix*				
		50 *Corvus monedula*	+			
1 ♀	H	*Corvus corone cornix*	+	26/1/55	Sjölunda	
		Corvus monedula				
		4000 *Fringilla*				
		800 *Chloris, Carduelis*	+ S			
		100 *Emberiza citrinella*				
		Plectrophenax				
1	H	*Corvus* (flocks)	+ S	3/2/55	Sjölunda	
		Fringilla (flocks)				
1	H	*Fringilla, Corvus*	+	6/2/55	Sjölunda	
		Corvus monedula				
1	H	*Fringilla*	+ S	8/2/55		
		Turdus				
4	H	*Fringilla, Emberiza*	+ S	14/2/55	Sjölunda	
		Plectrophenax				
1	H	*Fringilla* (flocks)	+	22/2/55	Sjölunda	
		Corvus corone cornix	+ M			
1	H	*Fringilla, Corvus*	+ S	28/2/55	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	(H)	(*Fringilla/Carduelis*) *Corvus, Larus*	+S	1/3/55	Sjölunda	
1	H	*Fringilla, Corvus*	+S	2/3/55	Sjölunda	
1	H	*Fringilla, Corvus Larus*	+S	7/3/55	Sjölunda	
1	H	*Fringilla, Carduelis* *Corvus*	+S +S	15/3/55	Sjölunda	
3	O	*Larus ridibundus* *Vanellus*	+S	7/4/55	Sjölunda	
1	H	*Calidris, Vanellus* *Larus ridibundus*	+ —	14/4/55	Sjölunda	
1	O	28 *Limosa lapponica* 250 *Calidris alpina* 12 *Totanus* 3 *Tringa* 86 *Sterna paradisaea*	+ + + + +	29/4/55	Sjölunda	
1	H	9 *Tringa*, 1 *Vanellus*	+	11/6/56	Sjölunda	
3	O, Sl	30 *Anas crecca*	+S	15/4/57	Börringe	B.C. & M.M.

AQUILA CHRYSAËTOS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1 juv.	H	*Columba palumbus*	+	5/1/47	Kongelund Amager	Denmark E.H.
1 juv.	H			11/10/47	Skanör	Hunting a hare S.U.
2 juv.	O	*Anser fabalis*	+S	6/10/48	Sövdesjön	
1 ad.	O	*Anser fabalis*	+S	6/10/48	Sövdesjön	
1 juv.	F	*Anser fabalis*	+S	31/10/48	Sövdesjön	
1 juv.	S	*Anser fabalis*	—	31/10/48	Sövdesjön	
1 juv.	H	*Anas* *Bucaphala clangula*	+	1/11/48	Sövdesjön	S.U.
1 juv.	O	*Mergus merganser*	+S	28/11/48	Sövdesjön	
1 juv.	H	*Anser fabalis*	+	20/2/49	Sövdeborg	G.R., M.M. & others.
1 juv.	Sl	*Corvus corone cornix*	(+)	29/1/50	Havgård, p. 106	A.E., N.T.-W. & M.M.
1 juv.	F	*Buteo buteo*	—	5/3/50	Sövdesjön	S.O.F. exc. A.E., K.G.W. & M.M.
2	F	1 *Accipiter nisus*	M	22/10/50	Börringe	S.O.F.
3 juv.	H	*Corvus*	+		S. Häckeberga	exc. A.E.
1 ad.	F	(1 *Aquila clanga*,				& M.M.

No.	Behaviour	Reacting species	Reaction	Date	Plate	Comments
		1 *Milvus milvus*)				
		1 *Falco tinnunculus*				
2 juv.	F	9 *Buteo buteo*	—	21/3/51	Börringe,	G.M. &
		1 *Accipiter gentilis*			p. 106	M.M.
3 juv.	F	8 *Buteo buteo*	—	5/3/52	Havgård,	O.M. &
		1 *Buteo lagopus*	—		p. 106	M.M.
		1 *Aquila clanga* (O)	—			
2 ad.	O	*Corvus corone cornix*	+	20/5/52	Stornäs	Lappland.
2 juv.	O	*Anser fabalis*	+	30/11/52	Börringe	L.S. & M.M.
3 juv.	F	*Corvus corone cornix*	—	14/2/54	Börringe	N.T-.W.,
		1 *Haliaeetus* (F)	—			G.M. & M.M.
1 juv.	F	1 *Buteo lagopus*	M	14/8/54	Sarektjåkko, p. 2090	Lappland G.M. & M.M.
4 juv.	F	2 *Haliaeetus albicilla*	—	28/10/54	Havgård, p. 106	Soaring
		1 *Falco tinnunculus*	—			
		3 *Buteo lagopus*	—			
		1 *Buteo buteo*	M			
1 juv.	O	1000 *Corvus*	+	21/1/55	Sjölunda	
		16,000 *Larus*				
		12,000 *Aythya, Bucephala*	+R			
		3000 *Anas*				
		Mergus				
1 ad.	S	3 *Corvus corone cornix*	F	18/3/56	S. Häckeberga	S.A.,
	T	*Corvus corone cornix*				G.M. & M.M.
3 juv.	H	*Anser fabalis*	+R	23/10/56	Benestad	
		Anas				
1 juv.	H	*Anser fabalis*	+S	20/10/56	Benestad	
1 juv.	S	1 ad. *Haliaeetus*	M	3/11/56	Sövde	(cf. *Haliaeetus*)
1 juv.	H	*Anas, Aythya, Mergus*	+R	11/1/57	Börringe	
		2 *Corvus corone cornix*	M			
1 juv.	O	*Corvus monedula*	(+)	11/1/57	Klågerup	
2 juv.	F	4 *Corvus corone cornix*	M	6/2/57	Havgård	B.C. & M.M.
1 juv.	H	*Anas, Mergus*	+	11/2/57	Hammarsjön	
1 juv.	O	*Columba*	+	17/2/57	Häckeberga	
	Sl, S	1 *Buteo buteo*	M			38 attacks
	T	*Buteo buteo*	—			

AQUILA CLANGA

No.	Behaviour	Reacting species	Reaction	Date	Plate	Comments
1	F	1 *Pandion haliaëtus*	—	20/9/49	Falsterbo	*Aquila clanga* or *aquila pomarina*

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	26 *Buteo buteo*	—	22/9/49	Falsterbo	G.O. & M.M.
1	O	*Buteo buteo* (many soaring)	—	29/9/49	Falsterbo	K-G.W. & M.M.
1	O	250 *Buteo buteo* (soaring)	—	4/10/49	Falsterbo	
1	O	*Corvus corone cornix*	—	22/10/50	Börringe, p. 106	A.E. & M.M.
1	H	*Corvus corone cornix* (4 *Aquila chrysaëtos*)	+	12/11/50	S. Häckeberga	S.O.F. exc. A.E. & M.M.
1	O	1 *Buteo buteo*	—		Börringe	S.O.F., G.R. & M.M.
1	O	1 *Larus (argentatus)* 1 *Accipiter nisus*	M	28/10/51	Falsterbo	*Aquila clanga* or *pomarina*
1	H	*Aythya, Bucephala* *Larus*	+ R	24/2/52	Sjölunda	Light, little & swift.
1	O	*Corvus*	+	8/10/53	Börringe Havgård, p. 106.	
1 juv.	H	*Larus argentatus* *Anas, Aythya*	+ R	21/1/54	Sjölunda	3 hunts.
1 juv.	S, T	*Corvus, Larus* *Anas*	+	21/1/54	Sjölunda	G.B.
1	H	*Aythya, Larus* 300 *Mergus albellus*	+ R	7/3/54	Sjölunda	
1	O	*Corvus corone cornix* 2 *Milvus milvus*	(+) —	28/3/54	Börringe	
1	F	1 *Aquila chrysaëtos* *Buteo buteo*	X	18/10/54	Börringe	Soaring togethher. E.H.
1	H	1000 *Anas platyrhynchos* *Larus* (flocks) *Corvus* *Mergus albellus* *Aythya, Anas*	+ R + R + + R	12/1/55	Sjölunda	The hunt was very energetic.
1	(H) H	(*Mergus albellus*) 3000 *Anas platyrhynchos* 2000 *Aythya, Bucephala* *Mergus* *Larus* (flocks)	+ R + + R + R	20/1/55	Sjölunda	
1	H	*Anas* (flock)	+ R	17/4/55	Häckeberga	S.A. & M.M.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	F	*Buteo* + 1 *Milvus milvus*	—	16/10/55	Falsterbo	On mig-ration. S.U.
2	O	4 *Buteo buteo*	—	18/3/56	Häckeberga	S.A., G.M. & M.M.
1	O	1 *Buteo buteo* (soaring)	—	18/3/56	Häckeberga	S.A., G.M. & M.M.
1	H	15–20 *Anas platyrhynchos*	+R	26/3/56	Häckeberga	S.A., O.M. & M.M.
2	O	*Anas*	+	1/4/56	Häckeberga	S.A.
1	H	*Anas platyrhynchos* + (flock) + *Aythya* *Mergus mergus*	+R + +	2/4/56	Häckeberga	S.A., G.M. & M.M.
1	O	1000 *Larus ridibundus* + *argentatus* 800 *Anas* + *Tadorna* *Tringa* *Vanellus*	+R + + +mW	11/6/56	Sjölunda	(*Aquila pomarina*)
1	O	8 *Anser fabalis* (S)	—	12/1/57	Havgård	
1	O	15–20 *Corvus corone cornix*	—	1/3/57	Havgård	
1	F	5 *Corvus corone cornix*	M	1/3/57	Havgård	Soaring.
1	O	4 *Buteo buteo*	—	7/4/57	Häckeberga	B.C. & M.M.

EAGLES SPEC.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	*Larus, Anas* *Mergus*	+	30/9/49	Falsterbo Måkläppen	Probably *Haliaetus*
1	O	*Larus, Anas*	+S	6/10/49	Måkläppen	Probably *Haliaetus*
1	F	*Buteo buteo* *Corvus corone cornix* } *Corvus monedula*	M M	5/10/52	Yddingen	*Aquila* S.O.F. exc.

BUTEO LAGOPUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	*Corvus monedula*	(+)	2/10/47	Lund, W.	Soaring low, cf. *Buteo buteo*
2	O	*Falco tinnunculus*	M	17/3/49	Krankesjön	A.E. & M.M.
1	O	*Falco tinnunculus*	+M	1/11/49	Havgård, p. 106	The kest-rel was mobbed by a sparrow hawk.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Corvus, Sturnus*	+S	8/3/50	Sjölunda	S.A. & M.M.
2	O	*Anas, Larus*	+	16/3/50	Sjölunda	S.A. & M.M.
1	F	*Turdus pilaris*	+S	26/11/50	Sjölunda	Migrating low.
1	O	*Corvus monedula*	+S	27/12/50	Lund W.	
2	(H)	*Alauda* (*Gallinula chloropus*)	+S	9/2/51	Sjölunda	
1	O	*Larus* (7–8000)	+			On migration.
		2 *Corvus corone cornix*	+M	17/3/51	Sjölunda	
		1 *Falco peregrinus*	+M			
		1 *Accipiter nisus*	M			
		2 *Asio flammeus*	+			
1	O	*Larus, Anas*	+S	31/3/51	Sjölunda	S.A. & M.M.
1	O	*Larus, Anas*	+	18/11/51	Sjölunda	
		Sturnus vulgaris *Corvus corone cornix*	+S	18/11/51	Sjölunda	
		Limosa lapponica *Calidris alpina* *Charadrius hiaticula* *Alauda arvensis*	+mE			
1	O	*Larus argentatus* *Larus marinus*	+R	21/1/52	Sjölunda	
6	O	*Larus, Anas*	+	13/10/53	Sjölunda	
1	O	*Corvus frugilegus* *Corvus monedula* (flocks)	+S	1/10/54	Ven	
2	O	*Corvus*	+S	2/10/54	Ven	
1	H	*Corvus, Larus, Anas*	+	10/1/55	Sjölunda	
1	H	*Corvus, Larus*	+S	14/2/55	Sjölunda	
1	O	*Corvus, Larus*	+S	18/2/55	Sjölunda	
1	O	*Larus, ridibundus* (flock)	+	11/6/56	Sjölunda	
		Vanellus (5–6)	+mW			
		Tringa (10–12)	+			
		Sterna	+			
1	F	*Larus canus* (S)	—	13/4/57	Sjölunda	
		Vanellus (S)	—			

BUTEO BUTEO

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
121	O	*Corvus monedula*	+	2/10/47	Lund	Soaring, partly low.
1	O	*Larus*	(+)	20/11/49	Sjölunda	The buzzards working hard in the wind. S.A. & M.M.
1	O	*Larus*	(+)	15/1/50	Sjölunda	
2	O	*Anas, Larus*	+	12/3/50	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	F	*Corvus* *Pica pica*	+S	28/12/50	Araslöv	
1	O	*Larus argentatus* 15 *Anas platyrhynchos* 24 *Anas penelope* 80 *Anas crecca* 8 *Anas clypeata* 50 *Tadorna* 30 *Numenius arquata* 200 *Calidris alpina* 4 *Corvus corone cornix*	+	22/4/50	Sjölunda	
1	F	3 *Vanellus vanellus* *Larus argentatus*	+M	25/2/51	Sjölunda	
31	O	*Larus* (7–8000) *Aythya, Bucephala* *Corvus corone cornix* *Vanellus vanellus*	+ + +M	17/3/51	Sjölunda	On migration.
1	O	*Larus, Anas*	+	31/3/51	Sjölunda	S.A. & M.M.
8	O	*Limosa lapponica* (75) *Haematopus*	+ +	15/4/51	Sjölunda	
10	O	5000 *Vanellus, Larus*	+S	28/9/51	Sjölunda	Soaring.
18	O	*Garrulus glandarius*	(+)	30/9/51	Revinge	
1	H	*Corvus monedula*	+S	19/1/52	Sjölunda	Real hunt.
29	O	*Corvus, Larus* *Limosa lapponica* *Calidris*	+	6/4/52	Sjölunda	
11	O	*Larus, Limosa*	—	6/4/52	Sjölunda	Soaring high.
4	O	*Larus ridibundus* *Larus argentatus* *Larus marinus* *Anas, platyrhynchos crecca*	+	11/11/52	Sjölunda	On migration low.
1	O	*Corvus corone cornix*	+S	25/12/52	Hammarsjön	
1	O	*Corvus corone cornix* *Corvus frugilegus* *Corvus monedula* *Fringilla, Carduelis*	(+)	23/12/53	Sjölunda	G.M. & M.M.
1	H	12 *Perdix perdix* 1 *Phasianus*	+	30/12/53	Sjölunda	
450	O	*Corvus frugilegus* *Corvus monedula* (flocks)	(+)/—	1/10/54	Ven	Buzzards on migration, flying high.
290	O	*Corvus monedula* (flocks)	+s/+	2/10/54	Ven	Flight low.
1	O	*Larus ridibundus* *Larus argentatus* (flocks)	+R	2/1/55	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
	H?	*Larus argentatus* (flocks)	+R	2/1/55	Sjölunda	No tendency to M behaviour.
30	2	*Corvus, Anas*				
		Larus (flocks)	+R	10/1/55	Sjölunda	
1	H	*Corvus, Larus* (flocks)	+	3/2/55	Sjölunda	
1	O	*Corvus, Larus* (flocks)	—	4/2/55	Sjölunda	
1	O	*Corvus monedula*	+S	8/2/55	Sjölunda	
		Fringilla				
20		*Corvus corone cornix*	+S	14/2/55	Sjölunda	
1	O	*Corvus corone cornix*	+S	28/2/55	Sjölunda	
1	H	*Corvus, Larus*	+S	8/3/55	Sjölunda	
1	O	*Corvus, Larus*	+S	13/3/55	Sjölunda	
1	O	*Larus*	+m	20/3/55	Sjölunda	
1	O, H	*Larus*	+mE	25/3/55	Sjölunda	
	H	100 *Vanellus*	+mE	25/3/55	Sjölunda	
6	O	*Larus ridibundus*	+	27/3/55	Sjölunda	
		Vanellus	+			
		Corvus	+mE			
1	O	8 *Corvus corone cornix*	+M	27/3/55	Sjölunda	
27	O	5000 *Larus ridibundus*	+, +mE	28/3/55	Sjölunda	
		10,000 *Larus argentatus*	+S			
		200 *Larus canus*	+S			
		Anas	+S			
		Vanellus	+			
1	O	*Haematopus*				
		Vanellus	+S	3/4/55	Sjölunda	
		Larus ridibundus				
6	O	*Larus argentatus*				
		Larus ridibundus	+S	6/4/55	Sjölunda	
		Vanellus	+, +m			
2	O	*Larus argentatus*	+m	7/4/55		
		Larus ridibundus				
28	O	*Larus, Vanellus*	+	8/4/55	Sjölunda	G.M. & M.M.
		Calidris, Anas				
1	O	*Larus, Anas*				
		Limosa, Numenius	+	13/4/55	Sjölunda	
		Calidris, Vanellus				
		Haematopus				
6	O	*Larus, Anas*				
		Limosa, Numenius	+	13/4/55	Sjölunda	
		Calidris, Vanellus				
		Haematopus				
		10 *Tadorna tadorna*	+			
3	O	10 *Larus ridibundus*	+	14/5/55	Sjölunda	
		2 *Larus minutus*	+			
		1 *Sterna hiruno*	+			
		80 *Sterna paradisaea*	+			

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		Tadorna	—			
		Tringa	—			
3	O	2000 *Larus (argentatus)*	+R	6/2/56	Sjölunda	Sl. some min. on a fence (a common behaviour for these species).
		500 *Corvus corone cornix*	+M			
		100 *Corvus frugilegus*	+M			
		100 *Corvus monedula*	+			
		10 *Plectrophenax*	+S			
		200 *Carduelis + Fringilla*	+S			
8	O	40 *Vanellus vanellus* (F)	+	25/3/56	Börringesjön	S.O.F., S.U. & M.M. Lapwings on migration deviated.
2	O	800 *Larus ridibundus*	+	28/3/56	Sjölunda	< 100 m above sea-level.
6	O	800 *Larus ridibundus*	—	28/3/56	Sjölunda	< 100 m above sea-level.
1	O	300 *Anas platyrhynchos*	+R	1/3/57	Björkesåkra	B.C. & M.M.
1	O	8 *Sturnus vulgaris*	+S	15/5/57	Åvarp	

CIRCUS CYANEUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	Passerine birds	—	14/9/47	Skanörs Ljung	
1 ♂	O	*Corvus corone cornix*	(+)	21/9/47	Romeleklint	
1 ♂	H	*Accipiter nisus*	M	24/9/47	Fyledalen	
3	H	*Carduelis* sp.	+	24/10/48	Häckeberga	
5	F	1 *Accipiter nisus*	+M	6/2/49	Havgård, p. 106	The 6 birds in a sort of play.
1	F	2 *Falco columbarius* ⎱ 1 *Accipiter gentilis* ⎰	M	8/10/49	Skanör	
		1 ad. *Accipiter gentilis*	—			
1	H	*Larus ridibundus*	+S	6/12/49	Löddeå	
1 ad.	H	*Corvus*				
		2 *Larus ridibundus* ⎱ 19 *Larus canus* ⎰ *Larus argentatus*	+	7/2/54	Lomma	
1	H	10 *Corvus corone cornix*	+	3/1/55	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments

CIRCUS AERUGINOSUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
2	O	*Vanellus vanellus*	+	30/5/47	Håslöv	40 *Vanellus.*
1	O	*Larus ridibundus*	+ M	14/6/47	Nymö	
2	H	*Larus ridibundus*	+ M	1/5/49	Yddingen	
1	H	*Anas querquedula*	+ S	5/5/49	Krankesjön	B.H.-C.
		Anas clypeata	+ S			& M.M.
1	O	*Anas, Aythya*	+	14/4/51	Sjölunda	S.A. &
		Larus, 125 Limosa lapponica	+			M.M.
		Tringa, Calidris	+ mE			
		Charadrius				
1	O	*Larus, Vanellus*	+	14/4/52	Sjölunda	
1	O	70 *Anas crecca*				
		6 *Anas clypeata*				
		1 *Anas penelope*				
		152 *Limosa lapponica*	+	9/5/54	Sjölunda	G.M. &
		1 *Numenius phaeopus*				M.M.
		500 *Calidris*				
		Tringa				

CIRCUS PYGARGUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Turdus* sp.	+ S	16/8/47	Stjärneholm	
1	H	*Larus ridibundus*	—	25/4/48	Krankesjön	
1	(H)	*Anthus*	+ S			
		(1 *Alauda arvensis*)		31/8/52	Falsterbo	(*Circus pygargus/ macrourus*) S.U., L.R. & M. M.
1	H	*Tringa* (flock)	+ S			
		1 *Limosa limosa*	+ m	14/5/53	Krankesjön	

MILVUS MILVUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O, H	*Corvus corone cornix*	+ M	9/8/47	Kungsmarken	*Milvus*
		Vanellus vanellus	+ M			on mig-
		Anas crecca	+ R			ration.
		Columba palumbus	+			
1	O	*Vanellus vanellus*	+ S	1/4/51	Löddeå	S.O.F. exc.
1	O	*Anas platyrhynchus*	+	2/4/56	(N.) Börringe	S.A.,
		25 *Anas crecca*	+			G.M. & M.M.
		1 *Capella gallinago*	+ S			Note!

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments

MILVUS MIGRANS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	*Larus ridibundus*	(+)	31/8/47	Oppmannasjön	
1	O	*Anas crecca*	+	7/9/52	Falsterbo Flommen	
1	F	2 *Falco subbuteo*	—	14/5/53	Krankesjön	

ACCIPITER GENTILIS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1 ad.	H	*Anas* sp.	+S	31/10/48	Sjölunda	
1 ad.	H	*Corvus corvus*	+	30/12/48	Döraberget (Skellefteå)	Väster-botten
1	H	*Emberiza citrinella* *Pica pica*	+	3/1/49	Döraberget (Skellefteå)	Väster-botten
1	O	*Corvus corone cornix* *Corvus monedula*	(+)	24/4/49	Snogeholmssjön	G.R. & M.M.
1	F	2 *Falco tinnunculus*	+M	19/9/49	Falsterbo	Did not migrate.
1	F	*Accipiter nisus*	+M	28/9/49	Falsterbo	Did not migrate.
		1 *Falco tinnunculus*	—	1/11/49		
1	O	*Parus* spec.	(+)	1/11/49	Havgård p. 106	Tits warned.
1	H	1 *Corvus corone cornix*	+	6/12/49	Barsebäcks fure	
1	O	*Corvus corone cornix* *Corvus*	+M	22/10/50	Barsebäcks fure	
1	F	Passerine birds *Vanellus vanellus* *Columba palumbus*	+	4/11/51	Bällinge ladu-gård	S.O.F. exc.A.E., T.H. & M.M.
1	O	1 *Accipiter nisus* 2 *Falco tinnunculus*	—	5/3/52	Havgård, p. 106	O.M. & M.M.
1	H	*Sturnus vulgaris* 1 *Falco tinnunculus*	+ +M	15/11/53	Havgård, p. 106	G.M. & M.M.
1	O	*Corvus monedula* (flocks) *Columba* (flock)	+ +	4/3/56	Lund N. + W.	Seen February toMarch.
1	H	*Corvus monedula* *Columba palumbus*	— +	23/10/56	Benestad	
1	O	*Columba palumbus*	—	17/2/57	Häckeberga	

ACCIPITER NISUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Chloris chloris* Passer	+S	21/11/48	Sjölunda	
1 ad.	H	*Pyrrhula pyrrhula* *Pica pica*	+ (+)	6/1/49	Lund	
1	H	*Motacilla alba + flava*	+S	13/9/49	Falsterbo	
1	H	*Motacilla alba + flava*	+S	15/9/49	Falsterbo	

	No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
I	1	H	*Calidris alpina*	+	21/9/49	Falsterbo	
I	1	H	*Calidris alpina*	+	21/9/49	Falsterbo	*Accipiter* migrated.
I	1	H	2 *Charadrius apricarius*	+	23/9/49	Falsterbo	
I	4	H	1 *Dendrocopus major*	+	24/9/49	Falsterbo	The
I	1	(H)	(*Dendrocopus major*)				woodpecker tried to escape by climbing on the lighthouse.
2	2	H	*Sturnus, Carduelis* et al. (150 birds)	+	29/9/49	Falsterbo	
I	1	H	25 *Anthus pratensis*	+	4/10/49	Falsterbo	Some specimens migrated.
I	1	H	1 *Carduelis spinus*	+	5/10/49	Falsterbo	
I	1	H	1 *Anthus pratensis*	+	5/10/49	Falsterbo	
I	3	H	18 *Carduelis spinus*	+	5/10/49	Falsterbo	
I	1	H	1 *Dendrocopus major*	+	5/10/49	Falsterbo	The woodpecker migrated.
I	1	H	1 *Pica pica*	+ M	5/10/49	Falsterbo	The hawk attacked first.
I	1	H	1 *Turdus*	+	11/10/49	Falsterbo	
I	1	H	*Sturnus vulgaris*	+	15/10/49	Sjölunda	S.A. & M.M.
I	1	H	*Sturnus vulgaris*	+	22/2/50	Sjölunda	
I	1	H	1 *Corvus corone cornix*	M	26/3/50	Yddingen	
I	1	O	*Anas, Larus*	—	4/4/50	Sjölunda	Soaring.
I	1	H	13 *Limosa lapponica* 41 *Numenius arquata* 3 *Recurvirostra* *Calidris* *Sturnus*	+ S	18/4/50	Sjölunda	
I	1	(H)	(*Calidris*)	S	19/5/40	Sjölunda	Surprise attack.
I	1	H	*Anthus pratensis*	+	30/9/50	Falsterbo	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
2	H	*Carduelis*	+	30/9/50	Falsterbo	The one
		Anthus, Motacilla ⎫	+	30/9/50	Falsterbo	hawk
3	H	*Carduelis* ⎭				hunting in vain for a long time.
1	H	*Anthus pratensis*	+ S	30/9/50	Falsterbo	
2	H	*Anthus*	÷	30/9/50	Falsterbo	
1	H	*Carduelis*	+	30/9/50	Falsterbo	
1	H	*Anthus*	+ S	30/9/50	Falsterbo	
1 + 1	H	*Anthus pratensis*	+	1/10/50	Falsterbo	
1	H	*Anthus pratensis*	÷ S	1/10/50	Falsterbo	2 attacks.
1	H	2 *Anthus pratensis*	÷ S	1/10/50	Falsterbo	3 + 1 attacks.
1	H	*Anthus pratensis*	+	1/10/50	Falsterbo	
1	H	*Anthus pratensis*	+ S	1/10/50	Falsterbo	2 attacks.
1	H	*Anthus pratensis*	÷	2/10/50	Falsterbo	9 attacks.
1	H	1 *Phylloscopus*	+ S	2/10/50	Falsterbo	
1	H	2 *Anthus pratenis*	÷	2/10/50	Falsterbo	
1	H	*Anthus pratensis*	÷	3/10/50	Falsterbo	3 attacks.
2	H	*Fringilla coelebs*	+	3/10/50	Falsterbo	5 + 3 attacks.
4	H	*Carduelis*	÷	3/10/50	Falsterbo	
1	H	*Antnus pratensis*	+ S	3/10/50	Falsterbo	
1	H	*Anthus pratensis*	+ S	5/10/50	Falsterbo	
1	H	*Fringilla coelebs*	÷	5/10/50	Falsterbo	1 attack.
1	H	*Anthus pratensis*	+ S	5/10/50	Falsterbo	
1	(H)	Passerine bird		6/10/50	Falsterbo	The hawk with a prey from a garden.
1	H	Passerine bird	+ S	11/3/50	Sjölunda	
1	H	*Calidris*	+			
	O	*Corvus corone cornix* ⎫	+ M	17/3/51	Sjölunda	
		Vanellus vanellus ⎭				
1	H	*Sturnus vulgaris* (1000)	+	1/4/51	Sjölunda	S.O.F. exc.
1	(H)	(*Turdus merula*)		1/4/51	Löddeå	S.O.F. exc.
1	O	*Limosa lapponica* ⎫	+ S	14/4/51	Sjölunda	S.A. & M.M.
		Calidris alpina ⎭				

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	*Limosa lapponica* (90)	+	15/4/51	Sjölunda	
		Haematopus ostralegus (16)	+			
1	H	*Motacilla*	+S	12/9/51	Falsterbo	
1	H	4 *Corvus corone cornix*	+M	28/9/51	Sjölunda	
1	H	*Corvus frugilegus*	M	28/9/51	Sjölunda	
1	H	*Fringilla*	+S	17/10/51	Falsterbo	
1	H	*Corvus corone cornix* ⎫ *Corvus frugilegus* ⎭	+M	24/10/51	Sjölunda	
3	H	*Sturnus vulgaris* ⎫ *Limosa lapponica* ⎬ *Calidris* ⎭	+	6/4/52	Sjölunda	
14	O–H	*Sturnus vulgaris* ⎫ *Limosa lapponica* ⎬ *Calidris* ⎭	+	11/4/52	Sjölunda	
		Vanellus vanellus	+S			
1	(H)	(*Sturnus vulgaris*)		11/4/52	Sjölunda	5 swoops.
1	(H)	(*Erithacus rubecula*)		21/9/53	Falsterbo	1 attack.
9	H	*Motacilla*	+S	28/9/52	Sjölunda	
2	H	*Carduelis, Fringilla*	+	12/10/52	Lomma	
1	H	*Calidris*	+S	4/10/53	Sjölunda	G.M. &
		Alauda				M.M.
9	O	*Larus ridibundus*	+S	13/10/53	Sjölunda	
		Tringa, Calidris	+S			
15	O–H	*Larus ridibundus*	(+)	25/10/53	Sjölunda	
1	(H)	(*Sturnus*)		25/10/53	Sjölunda	
1	H	*Fringilla, Carduelis*	+			
		Anthus pratensis	+S	23/12/53	Sjölunda	G.M. &
		Corvus monedula	(+)			M.M.
2	H	*Motacilla, Anthus*	+	7/4/54		
		Turdus				
1 ♀	H	*Larus ridibundus*	+			
		Larus canus ⎫ *Larus argentatus* ⎭	+S	7/4/54	Sjölunda	Long swoops.
1	H	*Fringilla*	+	8/2/55	Sjölunda	
		Corvus monedula				
1	H	*Emberiza citrinella*	+	11/2/55	Sjölunda	
		Fringilla				
1	H	*Fringilla, Chloris*	+S	25/2/55	Sjölunda	
		Larus (flocks)	+			
1	(H)	(*Fringilla*)	+	28/2/55	Sjölunda	1
	Sl	*Corvus* (flocks)	+			attack.
1	H	*Corvus, Larus*	+S	28/2/55	Sjölunda	
2	O	*Corvus, Larus*	+mE	1/3/55	Sjölunda	–
1	(H)	(*Carduelis/Chloris*)				
		Corvus, Larus	+mE			
1	H	*Carduelis, Corvus*	+S	8/3/55	Sjölunda	
1	O	*Corvus, Larus*	+S	15/3/55	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	1000 *Larus ridibundus*	+	17/3/55	Sjölunda	
		The *Larus r.* gave the alarm, before the hawk was visible to a human eye.				
		6000 *Larus argentatus*	+, +m		Sjölunda	
1	O, H	*Corvus monedula*	+	17/3/55	Sjölunda	
		Fringilla	+			
1	O	*Fringilla*	+ S	20/3/55	Sjölunda	
1	H	*Fringilla, Corvus*	+ S	23/3/55	Sjölunda	
		100 *Sturnus*	+ mW			
1	O, H	500 *Fringilla, Carduelis* } 50 *Anthus pratensis* }	+ S	27/3/55	Sjölunda	
		2000 *Larus ridibundus*	—			
		Larus ridibundus	+ S	6/4/55	Sjölunda	
		Vanellus				
6	O	*Larus*	+ S	7/4/55	Sjölunda	
		Vanellus				
4	O	*Larus*				
		Vanellus	+ S	8/4/55	Sjölunda	
		Calidris				
2	O	*Larus*	+	13/4/55	Sjölunda	
		Limosa lapponica	+			
		Calidris alpina	+			
		Vanellus vanellus	+			
		12 *Numenius arquata*	—			
2 juv. ad.	H	*Larus ridibundus*	+	18/4/55	Sjölunda	
		Larus argentatus	+			
		Larus argentatus	—			
		Limosa, Calidris	+			
		Totanus	+			
1	O	150 *Anas crecca*	+	20/4/55	Sjölunda	
		105 *Anas penelope*	+			
		48 *Limosa*	+			
		Calidris	+			
		Larus argentatus	—			
11	O	*Larus argentatus*	—	20/4/55	Sjölunda	
		48 *Limosa*	+			
		Calidris	+			
1	O	60 *Calidris*	+	26/4/55	Sjölunda	
		3 *Vanellus*	+			
2	O, H	300 *Larus ridibundus*	+	28/3/56	Sjölunda	A peregrine falcon had just captured a gull.
		Corvus (flock)	+			
		Sturnus (flock)	+			
		2 *Numenius arquata*	+			
		50 *Calidris*	+			
		38 *Totanus*	+			
1	H, S	13 *Larus*	+	13/4/57	Sjölunda	
		2 *Larus argentatus*	+			
		10 *Corvus monedula*	+ M			
1	O	*Larus*	M	13/4/57	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
		HALIAEETUS ALBICILLA				
1 juv.	S, F	*Corvus corone cornix*	M	21/1/47	Sjölunda	
	O	*Corvus corone cornix*	+			
		Anas platyrhynchos	+			1500 *Anas.*
		Mergus merganser	+R			
		Larus argentatus	+R			
1 ad.	O–H	*Larus ridibundus*⎫		17/1/48	Sjölunda	
		Larus canus ⎬	+R			
		Larus argentatus⎭				
		Anas platyrhynchos	+S			
3 juv.	O–H	*Anas platyrhynchos*	+S	29/2/48	Löddeå	
		Bucephala clangula	+S			
		Mergus merganser	+R			
3 juv.						
1 ad,	O	*Anser fabalis*	+S	6/10/48	Sövdesjön	
		1 *Clangula hyemalis*				
4	S, F	*Mergus merganser*	+S	12/12/48	Sövdesjön	
1 ad.	H	*Anas, Mergus merganser*	+R	16/12/48	Löddeå	
2	H	*Anser fabalis*	+	6/1/49	Sövdesjön	L.B., L.O. & S.U.
1 juv.	H	*Anas platyrhynchos*				
		Anas crecca	+R	13/1/49	Sjölunda	
		Anas penelope				
		Bucephala				
		Larus ridibundus				
		Larus argentatus	+R	13/1/49	Sjölunda	
1 juv.	O	*Anas, Larus*	+S	23/1/49	Sjölunda	
2 juv.	O	*Anas platyrhynchos*				
		Mergus meganser	+S	30/1/49	Sövdesjön	
1 ad.	S			13/2/49	Sjölunda	With prey. T.H. & S.U.
1	O	*Anas, Larus*	+S	27/2/49	Sjölunda	S.o.F. exc. Wet snow.
1 juv.	(H)	*Anas, Aythya*	+	17/3/49	Krankesjön	Swooped from 300 m and hit an *Anas* or a *Mergus.*
		Mergus meganser				
		Mergus albellus				
	S	2 *Corvus corone cornix*	M			
1 ad.	O	*Anser, Aythya,* ⎫				
		Bucephala ⎬	+S	25/3/49	Sövdesjön	
		Mergus merganser ⎪				
		albellus ⎭		25/3/49	Sövdesjön	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	*Anser + Anas*	+	26/3/49	Sövdesjön	L.B., L.O. & S.U.
1 juv.	H	*Buteo buteo* (on migration)		22/9/49	Falsterbo	Hunting *Buteo for* 2 min., then stooped.
1 juv.	F, Sl	*Anas*	+S	23/9/49	Skanör	
1 juv.	O	*Buteo buteo* (many soaring)	—	29/9/49	Falsterbo	
1	O	*Buteo buteo* (many soaring)	—	4/10/49	Falsterbo	Migrated.
1 ad.	H	12 *Ardea cinerea* *Anas*	+	6/12/49	Löddeå	
2	S	*Anas, Mergus*	—	19/2/50	Börringe	The eagles on the ice.
1 ad.	O	1 *Buteo lagopus* 2 *Larus Canus*	M	19/8/50	Jetnam	SW. Lappland.
1	O	*Anas platyrhynchos* (2500)	R	31/1/51	Sjölunda	No. 1.
		Latus ridibundus, Canus	+R			
		+ argentatus (6000)	+R			
		1 *Falco peregrinus*	+M			
		1 *Buteo buteo*	+			
	Sl–S	*Corvus corone cornix*	M			
		Bucephala				
1	O	*Anas + Aythya*	+R	31/1/51	Sjölunda	No. 2.
		Larus	+R			
		Corvus	+			
	Sl. S	40 *Corvus corone cornix*	M			
1	H	*Larus + Anas + Aythya*	+R	31/1/51	Sjölunda	No. 3 (3 sea eagles).
		Bucephala				
		Corvus	+			
1 juv.	O	*Anas, Aythya* *Larus*	+R	4/3/51	Sjölunda	
1	O–H	*Larus argentatus* *Anas* *Aythya*	+R			G.M. & M.M.
				22/3/51	Sjölunda	
		11 *Corvus corone cornix*	+			
		Numenius + Vanellus	+			
1	O	*Anas, Mergus*	+	24/3/51	Araslövssjön	G.M. & M.M.
1	O	*Anas, Mergus, Aythya*	+	25/3/51	Araslövssjön	G.M. & M.M.
		Larus	+			
		Vanellus vanellus	+M	2/11/51	Sjölunda	
	H	*Vanellus vanellus*	+			
1 juv.	H	*Anas*	+	6/12/52	Sövde	S.U.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1 juv.	(H)	(*Anser fabalis*)	O	6/12/52	Sövde	S.U.
1 ad.	F	*Mergus merganser*	(+)	13/1/52	Sövde	A.E., G.R. S.U., & B.H.C.
4 juv.	F	3 *Buteo buteo*	—	5/3/52	Börringe	O.M. & M.M.
1 juv.	O	*Vanellus vanellus* (flock)	+mE	5/3/52	Börringe	O.M. & M.M.
1 ad.	F	*Buteo lagopus*	+M	25/7/52	Jetnam	Lapp-land.
		Pandion haliaëtus	+M			
1 ad.	O	*Corvus corone cornix*	+	23/2/52	Emilstorp (Malmö)	
		Vanellus vanellus (small flocks)				
1 juv.	O	10 *Cygnus colombianus*	(+)?	15/11/53	Havgård	The flying swans altered their direction almost 90°. G.M. & M.M.
1 juv.	H	*Anas (plat.)* 10,000 *Aythya* 1000 *Bucephala* 200 *Somateria* *Larus*	+R	28/2/54	Sjölunda	G.M. & M.M.
2	H	*Aythya, Bucephala*	+R	7/3/54	Sjölunda	
1	H	5000 *Aythea, Bucephala* 1000 *Anas platyrhynchos* 3000 *Larus* *Mergus*	+R	21/3/54	Sjölunda	L. Svens-son & M.M.
1	O	22 *Vanellus vanellus*	(+)	28/3/54	Börringe	The lap-wings altered their course.
1	O	50–60 *Buteo buteo*	—	3/10/54	Yddingen	400 soar-ing buz-zards on migra-tion. A.E., T.H. & M.M.
3	F	1 *Corvus corone cornix/moned.*	+	28/11/54	Saxtorps fure.	Sk. O.F. exc.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	H	2000 *Anas platyrhynchos*	+R	7/1/55	Sjölunda	
		6500 *Aythya*	+S			
		16,000 *Larus*	+R			
1	H	17,000 *Larus*	+R	12/1/55	Sjölunda	
		Anas (flocks)	+			The gull
	(H)	(*Larus argentatus*)				was in-
						jured.
1	H	17,000 *Larus*				
		Anas, Aythya	+R	4/2/55	Sjölunda	
		90 *Mergus albellus*				
		100 *Corvus*	+			
		200 *Fulica*	(+)			
		Cygnus cygnus	—			
1	H	*Larus, Anas*	+R	5/2/55	Sjölunda	
		Mergus				
		Corvus	+			
		Aythya	(+)			
1	O	*Bucephala*	(+)	13/2/55	Falsterbo	L.R.,
						E.Sv. &
						M.M.
2 ad.	H	*Larus* (flocks)	+	17/2/55	Sjölunda	E. Salé
2 ad.	H	*Larus, Anas*	+R	19/2/55	Sjölunda	
1 juv.	H	*Corvus*	+			
3	H	5000 *Larus argentatus*	+R			
		2000 *Aythya*				
		1500 *Corvus*	+			
		Mergus	+			
1 ad.	H	1000 *Anas platyrhynchos* ⎫	+R	23/2/55	Sjölunda	
		8000 *Larus argentatus* ⎭				
	H	*Mergus, Aythya*	+			
		300 *Anas*	—			
2	O	15,000 *Larus*	+R	23/2/55	Sjölunda	S.A.,
		Anas	+			A.E. &
		Corvus	+			M.M.
1 ad.	H	60–70 *Anas platyrhynchos*				
		Crecca	+R	27/2/55	Häckeberga	S.A.,
						A.E. &
						M.M.
1 juv.	O	1 *Buteo buteo*	—			
1 juv.	H	3000 *Anas platyrhynchos* ⎫				
		2 *Anas crecca* ⎬	+R	5/3/55	Sjölunda	
		25 *Tadorna* ⎭				
		1000 *Larus*	+, +mE			
1 juv.	F	15 *Buteo buteo*	—	2/4/55	Börringe	G.M. &
						M.M.
1 juv.	O	*Larus*	+	12/1/56	Sjölunda	G.B.
1 juv.	O	*Larus argentatus*	+R	26/1/56	Sjölunda	
		Larus marinus				

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1 ad.	H	10–15,000 *Larus argentatus*	+R	27/1/56	Sjölunda	
		800 *Larus marinus*	+			
		400 *Anas platyrhynchos*	+R			
		Aythya	+			
		Mergus	?		(Segeå)	
1 ad.	O	15,000 *Larus* (flocks)	+R	6/2/56	Sjölunda	
	(H)	*Larus* (flocks)	+mE			
		Mergus, Aythya	+S			
		Anas	+			
		700 *Corvus* (1)	+S			
		Corvus (2)	+mE			
4 juv.	S	15–20 *Corvus corone cornix*	S	2/3/56	Börringe	On the ice. E. Sv. & M.M.
1 ad.	F	*Corvus corone cornix*	+S			E.Sv., G.M. & M.M.
4 juv.	S, F	18 *Corvus corone cornix*	(+)	4/3/56	Börringe	
1 ad.	F (H)	*Anas crecca* (flock)	F	18/3/56	Häckebergasj.	S.A., G.M. & M.M.
1 ad.	O	600 *Corvus corone cornix*	+	28/3/56	Sjölunda/Lomma	
		2000 *Anas*	+			
		5000 *Larus*	+			
		Tringa	—			
2 ad.	F	*Rissa* + *Alcae*	(+) —	17/8/56	Veddöy	G.M. & M.M.
3 juv.		*Larus argentatus*			Röst (Norway)	
1 ad.	(H)	(*Somateria molissima*)				
1 juv.	O	3 *Corvus corone cornix*	M	23/10/56	Ilstorp	
1	O	200 *Anser fabalis*	(+)	3/10/56	Karup	High. G.M. & B.B.
1	O, Sl	*Anser fabalis*	+S	3/10/56	Karup	Low (15 m). G.M. & B.B.
	T	200 *Anser fabalis*	(+)			
1 juv.	H	400 *Anas platyrhynchos*				
		75 *Anas penelope*				
		50 *Anas crecca*	+S	3/11/56	Sövdesjön	
		Aythya				
		Mergus merganser + *albellus*				
1 ad.	S 1 juv.	*Aquila chrysaetos*	M	3/11/56	Sövde	(Cf. *Aquila*)
1 ad.	H	*Anser fabalis*	S	25/12/56	Araslövssjön	
1 juv.	H	*Anas platyrhynchos*	+			
		Corvus	+S			

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
3 juv.	O	Anas, Aythya Bucephala Mergus	+ S	11/1/57	Börringe	
2 ad. 2 juv.	F, Sl	Mergus (flock)	—	12/1/57	Börringe	
2 ad.	F	Mergus merganser Mergus albellus Bucephala	— (+) (+)	25/1/57	Våmbsjön	
2 juv.	H	500 Anser 1000 Anas, Mergus	+ S + m	10/2/57	Hammarsjön	
2	H	2000 Anser fabalis	+ R	16/3/57	Sövdesjön	B.B., G.M. & M.M.

PANDION HALIAËTUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
2	O, F	2 Accipiter nisus Anas crecca	+ S + S	10/8/47	Löddeå	
	Sl, S	Anas crecca	—			
1	F	Laris ridibundus Sterna sp.	—	22/8/47	Yddingen	
1	O	66 Limosa lapponica Larus	+	8/4/50	Sjölunda	
1	O	1 Limosa limosa 60 Numenius Larus	+ S	9/4/50	Sjölunda	
1	O	1 Corvus corone cornix 2 Corvus monedula 4 Pica pica Anas (flock) Tadorna (flock) Numenius arquata Limosa lapponica	+	11/4/52	Sjölunda	
1	O	70 Aythya 21 Anas 60 Larus ridibundus	+ S	19/5/52	Furunäsviken (Skellefteå)	G.M. & M.M.
1	O	Anas, Larus 3000 Vanellus	+ +	2/9/52	Sjölunda	
1	O	Larus ridibundus, argentatus Anas, Tadorna Vanellus 250 Calidris alpina	+ + +, +mE +	6/4/55	Sjölunda	
1	O	Larus ridibundus Larus argentatus Larus, Vanellus	+ mE	7/4/55	Sjölunda	
		Calidris, Anas	+	8/4/55	Sjölunda	
3 (1 + 1 + 1)	O	10–15,000 Larus argentatus 3000 Larus argentatus (+ Larus ridibundus)	+ R + mE	25/4/56	Sjölunda	

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments

ARDEA CINEREA

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
2	F, Sl	300 *Larus ridibundus*	+S	1/6/50	Sjölunda	
3	F, Sl	*Anas platyrhynchos* *Anas crecca*	+S	19/11/50	Sjölunda	
1+2	O	*Anas, Tadorna*	+S	18/3/51	Sjölunda	S.O.F. exc. (see *Falco peregrinus*).
1	F	50 *Anas crecca* 4 *Anas clypeata* 8 *Anas penelope*	+S	21/4/51	Sjölunda	
2	O	1000 *Larus ridibundus* 10 *Larus canus* 800 *Larus argentatus* 1 *Larus fuscus* 10 *Larus marinus*	—	16/4/52	Sjölunda	High.
1	T	*Larus* (mixed flocks)	+R	16/2/52	Sjölunda	
6	O	*Larus*	—	13/10/52	Sjölunda	Low.
1	O	*Larus*	+S	13/10/52	Sjölunda	
2	T	*Larus ridibundus*	+S	25/10/53	Sjölunda	
1	Sl	*Larus ridibundus* *Larus argentatus* *Corvus* *Mergus albellus* *Tadorna tadorna*	−S (+)	13/2/55	Sjölunda	A.E., T.M. & M.M.
1	T	*Larus, Corvus*	(+)	14/3/55	Sjölunda	
1	O, Sl	100 *Anas platyrhynchos* *Aythya* *Mergus merganser*	+S +S +	25/12/56	Hammarsjön (Ekenabben)	
1	Sl	*Anas, Aythya* *Mergus*	+S	26/12/56	Hammarsjön (Ekenabben)	
1 juv.	O	22 *Larus ridibundus* 30 *Larus argentatus*	+S +S	27/5/57	Gedser	(Denmark)
1	O	18 *Larus argentatus* 30 *Larus argentatus* 22 *Larus ridibundus*	−− + −−	27/5/57	Gedser	Induction.
1	O	> 90 *Corvus corone cornix* *Corvus monedula*	+	3/3/59	Ilstorp	G.M. The heron was flying low.

CICONIA CICONIA

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	*Anas, Larus* *Limosa, Numenius* *Tringa, Vanellus* *Haematopus* (*Calidris?*)	+	19/4/52	Sjölunda	The storks were flying high.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments

GRUS GRUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
3	O	*Larus* (flocks)	+	11/6/56	Sjölunda	
		700 *Anas* + *Tadorna*	+			
		6 *Hydroprogne*	—			
		155 *Sterna*	—			
		Vanellus	+			

BOTAURUS STELLARIS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	F, Sl	*Anas* spec. *Larus ridibundus* *Chlidonias niger*	+S	13/5/47	Håslöv	K.G.W. & M.M. The bittern flew some 30 m.
1	F, Sl	*Chlidonias niger*	—	13/5/47	Håslöv	

PERNIS APIVORUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	200 *Limosa lapponica* 1000 *Calidris alpina* 30 *Charadrius hiat.* *Larus, Anas*	+	14/5/51	Sjölunda	
1	O	108 *Tadorna tadorna* 135 *Calidris alpina* *Larus*	+S	22/5/55	Sjölunda	

CUCULUS CANORUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	*Corvus monedula*	M	27/5/55	Sjölunda	G.M.

CORVUS CORONE CORNIX

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	F	13 *Limosa lapponica* 7 *Numenius arquata* 2 *Mergus merganser*	+S	17/4/51	Lomma	S.A.
1	O	16 *Tringa erythropus*	+S	10/5/52	Furunäsviken (Skellefteå)	G.M. & M.M.

VANELLUS VANELLUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
2	O	*Larus argentatus* + *ridibundus*	+	1/4/55	Sjölunda	The lapwings on migration at a great height descended over the locality.

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments

STERNA ALBIFRONS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	M "H"	170 *Calidris*	+	29/4/50	Sjölunda	30 m from nest.

LARUS ARGENTATUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	O	32 *Plectrophenax nivalis*	(+)	21/1/50	Sjölunda	Warned.

LARUS RIDIBUNDUS

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
1	M!	*Apus apus*	+	25/5/57	Lund	Deviated.

PHALACROCORAX CARBO

No.	Behaviour	Reacting species	Reaction	Date	Place	Comments
3	O	*Corvus monedula*	(+)?	26/6/54	Lund	

APPENDIX II

INDUCTION

(Contagious Reaction)

Disturbance or cause	Primary reaction		Sec. reaction		Date	Place
Homo	50 *Larus ridibundus*	+	32 *Limosa lapponica*	+	4/4/50	Sjölunda
			58 *Numenius arquata*	+		
Homo	*Tringa, Charadrius*	+	*Calidris*	+	25/4/50	Sjölunda
Cygnus olor in migratory restlessness.	62 *Cygnus olor*	T	*Limosa lapponica* / *Tringa,* / *Calidris*	+	26/4/50	Sjölunda
Homo	200 *Limosa lapponica*	+	360 *Calidris alpina*	+	30/4/50	Sjölunda
			Calidris canutus	+	30/4/50	
Homo	*Tringa totanus*	+	9 *Calidris ruficollis*	+m	19/5/50	Sjölunda
			4 *Calidris temminckii*	+m		
Falco peregrinus.	*Anas platyrhynchos* *Larus argentatus*	+R	400 *Fringilla,* *passer, Chloris*	+S	23/2/55	Sjölunda
"The arm test."	*Larus argentatus* *Larus ridibundus*	+	200 *Fringilla monti-fringilla*	+S	23/2/55	Sjölunda
Pandion	*Larus,* *Anas* et al.	+	10 *Tadorna tadorna*	+S	13/4/55	Sjölunda
Milvus	*Anas*	+	1 *Capella gallinago*	+S	2/4/56	Börringe
Ardea cinerea	18 *Larus argentatus*	+	30 *Larus argentatus*	+	27/5/57	Gedser
			22 *Larus ridibundus*	+		

DISTURBANCE NOT OBSERVED, NOT LOCALIZED OR NOT DEFINED

No.	Reacting species	Reaction	Date	Place	Probable cause
	Larus ridibundus	+S	13/5/47	Vejlasjön	4 violent risings (fox?).
	Larus ridibundus, canus				
10,000	*Larus argentatus*	+	8/3/50	Sjölunda	S.A. & M.M.
	Larus marinus				
	Anas, Larus				
98	*Haematopus ostralegus*	+	27/3/50	Sjölunda	S.A. & M.M.
	Larus (flocks)	+	15/4/50	Sjölunda	—
72	*Vanellus vanellus*	+(R)	15/4/50	Sjölunda	(*Falco?*)
	Larus, Vanellus	+	30/4/50	Sjölunda	*Phalacrocorax?*
	Larus (flocks)	+	16/9/51	Falsterbo	(*Haliaeetus?*)
3000	*Corvus corone cornix* (flock) / *Vanellus vanellus* / *Larus* (flock)	+	6/10/51	Sjölunda	(*Falco?*)
	Larus, Corvus	+	17/2/52	Sjölunda	*Falco peregrinus* was seen later.

No.	Reacting species	Reaction	Date	Place	Probable cause
600	Larus ridibundus				
	Larus canus	+	9/3/52	Sjölunda	(Falco?)
1000	argentatus, Larus				
100	Larus marinus				
500	Anser fabalis	+	9/11/52	Höjeå	(Fox?)
270	Sterna paradisaea	+S	3/5/54	Sjölunda	—
14	Larus minutus				
3	Arenaria interpres	+	3/5/54	Sjölunda	
	Tringa, Calidris				
	Larus ridibundus, canus	+	7/12/54	Sjölunda	(Falco?)
	Larus argentatus, marinus (flocks)				
	Aythya, Bucephala (flocks)	+S	6/1/55	Sjölunda	—
10,000	Larus	+	12/1/55	Sjölunda	
	Corvus, Anas, Larus	+	14/1/55	Sjölunda	(Falco?)
	Larus, Corvus	+	17/1/55	Sjölunda	(Falco?)
35	Turdus pilaris	+			
1	Capella media	+S	19/1/55	Lomma	(Cat?)
	Larus, Anas	+	20/1/55	Sjölunda	(Falco?)
1000	Larus	+R			
	Anas, Mergus	+	4/2/55	Sjölunda	(Falco?)
	Larus	+	15/2/55	Sjölunda	—
130	Anser fabalis	+	26/2/55	Trelleborg	—
	Larus, Corvus	+	1/3/55	Sjölunda	—
	Larus, Corvus	+	9/3/55	Sjölunda	—
	Larus	+	26/1/56	Sjölunda	—
	Anas, Tadorna	+	20/4/56	Sjölunda	—
10–15,000	Larus	+R	6/2/56	Sjölunda	

AIRPLANES

No.	High	Low	Reacting species	Reaction	Date	Place	Comments
1		×	Larus, Anas	+	22/4/50	Sjölunda	All birds save swans.
			Tadorna, Numen.				
			Calidris				
			Passerine birds				
			Larus, Anas				
1		×	Somateria	+	21/9/53	Falsterbo	(Måkläppen.)
1	×		Larus, Anas	?(+S)	31/1/54	Sjölunda	Far away.
			Mergus				
1		×	Anas platyrhynchos				
			Tadorna				
			4000 Aythya	+	15/3/55	Sjölunda	
			2 Vanellus				
			100 Corvus				
			2000 Larus				

No.	High	Low	Reacting species	Reaction	Date	Place	Comments
1		×	*Larus* (flocks)	+S	19/3/55	Sjölunda	Air liner.
1		×	*Anser fabalis*	+S	29/3/55	Arlövs ängar	
2		×	*Anas, Larus,* *Vanellus, Calidrius*	+			
1		×	100 *Anas crecca*	+	15/4/55	Sjölunda	G.M. &
			38 *Limosa lapponica*	+			M.M.
			Larus	—			
			Anas platyrhynchos	—			
1		×	*Anas, Tadorna*	+	29/4/55	Sjölunda	
			Limosa	+			
			Totanus, Tringa	+S			
			Sterna	+S			
1	×		*Larus* (flocks)	+R	6/2/56	Sjölunda	Sporting
			Corvus (flocks)	+			aircraft.
1		×	900 *Somateria molissima*	+S	5/4/57	Sjölunda	
			50 *Somateria molissima*	+m			

"THE EAGLE TEST" ("THE ARM TEST")

No.	Reacting species	Reaction	Date	Place	Comments
10	*Philomachus pugnax*	+S	20/6/47	Sjölunda	
2	*Hydroprogne tschegrava* (M)	+S	12/7/47	Lau, Gotland	
	Ardea cinerea	+	25/3/48	Löddeå	
8000	*Aythya*	+	5/2/50	Sjölunda	
3	*Anser anser*	+	16/4/50	Löddeå	S.U. & M.M.
1	*Calidris ruficollis*				
6	*Calidris temminckii*	—	20/5/50	Sjölunda	
1	*Limicola falcinellus*				
2	*Tringa hypoleukos*				
2	*Tringa glareola*	+S	20/5/50	Sjölunda	
1	*Calidris ferruginea*				
1	*Calidris canutus*	—	20/5/50	Sjölunda	
38	*Chlidonias niger*	+S	22/5/50	Sjölunda	
1	*Numenius phaeopus*	+m	22/5/50	Sjölunda	
2	*Arenaria interpres*	+S	22/5/50	Sjölunda	
3	*Limicola falcinellus*	—	27/5/50	Sjölunda	1 bird warned.
650	*Anas platyrhynchos*	+S	2/6/50	Sjölunda	
19	*Calidris alpina*				
2	*Calidris ferruginea*	—	2/6/50	Sjölunda	Did not even react for
2	*Limicola falcinellus*				man.
2	*Numenius phacopus*	+	28/6/50	SE. Dåkkejaure	(Lappland)
2	*Stercorarius longicaudus* (M)	+	30/6/50	Bosjusjaure	(Lappland)
12	*Calidris temminckii*				
6	*Arenaria intrepres*				
12	*Larus canus +fuscus*	+	16/7/50	Medgrund (SE. Skellefteå)	G.M. & M.M.
6	*Larus argentatus*				
21	*Sterna paradisaea*	+S	16/7/50	Medgrund (SE. Skellefteå)	G.M. & M.M.

No.	Reacting species	Reaction	Date	Place	Comments
6	*Chlidonias nigra*	+ S	10/5/51	Sjölunda	
250	*Sterna paradisaea*				
102	*Limosa lapponica*	+ S	10/5/51	Sjölunda	
11	*Larus minutus*	+ S	12/5/51	Sjölunda	The gulls warned at a great distance.
540	*Limosa lapponica*	+ S			
1000	*Calidris alpina*	+			
22	*Tringa glareola*	+ m	18/5/51	Sjölunda	
14	*Tringa glareola*				
>3000	*Fulica atra*	(+)	20/9/51	Sjölunda	
6000	*Vanellus vanellus*	+			
1500	*Charadrius apricarius*	+			
1	*Limosa limosa*	+ S			
1	*Philomachus*	+			
6	*Capella*	+ S	24/11/51	Sjölunda	A.E. & M.M.
16	*Calidris alpina*	+			
	Anas, Larus	+			
	Larus ridibundus	+ R			
10	*Haematopus*	+	13/4/51	Sjölunda	
2	*Larus minutus*				
1000	*Larus ridibundus*				
50	*Larus canus*	+	23/5/52	Sjölunda	
400	*Larus argentatus*				
800	*Anas crecca*				
200	*Anas platyrhynchos*	+	31/8/52	Sjölunda	
	Anas penelope				
1000	*Vanellus*				
100	*Philomachus*				
1000	*Calidris*	+	31/8/52	Sjölunda	
50	*Charadrius*				
100	*Corvus corone cornix*				
8	*Corvus frugilegus*				
40	*Corvus monedula*	+	3/11/52	Sjölunda	
15	*Sturnus vulgaris*				
9	*Pica pica*				
	Passer chloris	—			
29	*Mergus albellus*	+ R	21/12/52	Sjölunda	
3000	*Aythya*	+ S	21/12/52	Sjölunda	
5	*Corvus corone cornix*				
11	*Corvus frugilegus*				
100	*Corvus monedula*	+	3/5/53	S. Sjölunda	
2	*Pica pica*				
100	*Sturnus vulgaris*				
1000	*Larus ridibundus*				
1	*Larus minutus*	+	16/5/53	S. Sjölunda	
8	*Chlidonias nigra*				
4	*Sterna hirundo*				
70	*Sterna paradisaea*	+ S	17/5/53	S. Sjölunda	
4	*Sterna albifrons*				

No.	Reacting species	Reaction	Date	Place	Comments
1	*Calidris alpina*	—	30/12/53	S. Sjölunda	The dunlin evidently was in good condition.
6	*Asio flammeus*	+	3/1/54	S. Sjölunda	G.M. & M.M.
3	*Tringa totanus*	+S	21/2/54	Lomma	
17	ad. *Larus minutus,*				
3	juv. *Larus minutus,*	+S	4/5/54	Sjölunda	
3	*Chlidonias nigra*				
600	*Sterna paradisaea*				
	Larus (flocks)	+	9/5/54	Sjölunda	G.M. & M.M.
18	*Calidris temminckii*	—	12/5/54	Sjölunda	
14	*Haematopus*	+mE	12/5/54		
100	♂♂ *Anas platyrhynchos*				
4	*Anas clypeata*	+	28/5/54	Sjölunda	Swimming.
1	*Anas querquedula*				
53	*Pinicola enucleator*	—	21/11/54	Lomma	
90	*Bombycilla garrulus*	—	21/11/54	Lomma	
250	*Turdus pilaris*	+	21/11/54	Lomma	
6	*Pinicola enucleator*	—	28/11/54	Lomma	Sk.O.F. exc.
15,000	*Larus argentatus*				
200	*Larus marinus*				
1000	*Larus ridibundus*	+R	5/1/55	Sjölunda	
13	*Larus canus*	+S	5/1/55	Sjölunda	Apathetic because of the cold.
15,000	*Larus argentatus*				
>1000	*Larus marinus*				
3–4	*Larus canus*	+R	11/1/55	Sjölunda	3 times at a *distance of at least 1000 m.*
>1000	*Larus ridibundus*				
16,000	*Larus*	+R			
5000	*Corvus monedula*				
<100	*Corvus corone cornix*	+	17/1/55	Sjölunda	
31	*Pica pica*	+	19/1/55	Sjölunda	
35	*Mergus albellus*				
5	*Mergus merganser*	+R			
	Aythya	(+)	20/1/55	Sjölunda	4 tests positive.
	Larus (flocks)	+R			
800	*Anas platyrhynchos*	+R	23/2/55	Sjölunda	S.A., A.E. & M.M.
500	*Larus argentatus*				
	Larus ridibundus	+	24/2/55	Sjölunda	
200	*Fringilla montifringilla*	—	24/2/55	Sjölunda	
	Fringilla montifringilla	+S	24/2/55	Sjölunda	Positive reaction, induced by the gulls.
1	*Mergus albellus* ♂	(+)	26/2/55	Höjeå	Swimming away.
500	*Corvus, Pica pica*	+			
3000	*Larus*	+, +mE	2/3/55	Sjölunda	Test with 1 arm only, distance 500 m.
5000	*Anas*	+S			
9000	*Larus*	+, +mE	9/3/55	Sjölunda	
200	*Corvus corone cornix*	+S	22/3/55	Sjölunda	
12	*Corvus frugilegus*	+S	22/3/55	Sjölunda	

No.	Reacting species	Reaction	Date	Place	Comments
200	*Corvus monedula*	+mE			
100	*Sturnus vulgaris*	+S			
< 100	*Corvus*	+	23/3/55	Sjölunda	
2000	*Sturnus*	+S			
1000	*Sturnus*	+mW			Note W.
73	*Haematopus,*				
4	*Tringa totanus,*	+S	3/4/55	Sjölunda	
	Vanellus				
	Larus (flock)	+, +m	13/4/55	Sjölunda	
	Anas (flock)	+			
	Tadorna	+			
	Limosa (flock)	+			
	Numenius (flock)	+mE			
	Calidris (flock)	+			
	Totanus (flock)	+			
	Vanellus (flock)	+			
24	*Haematopus*	+			
20	*Larus ridibundus*	+	19/5/55	Sjölunda	150 m. G.M.
22	*Sterna paradisaea*	+			150 m. G.M.
120	*Tadorna*	(+)+S			
	Tringa totanus	—			< 150 m. G.M.
12	*Larus fuscus*	+	5/7/55	Kågnäsudden	Västerbotten
8	*Larus fuscus*	+	20/7/55	Snusan	Västerbotten
50	*Sterna paradisaea*	+			G.M., A.S. & M.M.
4	*Sterna hirundo*	+S			
2	*Numenius phaeopus*	+mE			
100	*Rissa tridactyla*	+	30/7/55	Vardø	Varanger
1000	*Rissa tridactyla*	+	30/7/55	Vardø	Varanger
200	*Larus argentatus*	+			A.S. & M.M.
400	*Rissa tridactyla*	+	2/8/55	Berlevåg	Varanger
	Rissa tridactyla	+	2/8/55	Berlevåg	Varanger
	Larus argentatus + *Larus marinus*	+			
10,000	*Larus argentatus*	+R	6/2/56	Sjölunda	
500	*Larus marinus*	+R			
400	*Larus ridibundus*	+			
12	*Larus canus*	+			
700	*Corvus*	+			
1	*Buteo lagopus*	(S)—	6/2/56	Sjölunda	40 m.
1	*Buteo buteo*	(S)—	6/2/56	Sjölunda	40 m.
	Larus (flocks)	+R	4/3/56	Sjölunda	300 m.
	Corvus (flocks)	+			S.O.F., A.E. & M.M.
22	*Vanellus*	+	5/4/57	Sjölunda	Teacher pointing with a rod.
1	*Numenius*	+			
	Calidris	+			
50	*Sturnus*	+S			
	Larus ridibundus	+			

No.	Reacting species	Reaction	Date	Place	Comments
80	*Somateria molissima*	+ (deviating)			
	Larus (flocks)	+R	11/4/57	Sjölunda	
	Anas (flocks)	+			
74	*Numenius arquata*	+			
	Calidris, Vanellus	+	15/4/57	Sjölunda	
	Haematopus	+			
	Larus, Sterna	+	29/4/57	Sjölunda	

SHOOTING

Number of shots before reaction		Reacting species	Reaction	Date	Place	Comments
		Larus	+			
		Anas platyrhynchos, crecca				
1	3	*Anas acuta*				
	24	*Numenius arquata*	+mE	30/3/50	Sjölunda	
	2	*Numenius phaeopus*				
	43	*Calidris alpina*				
	41	*Vanellus vanellus*				
	37	*Tadorna tadorna*				
2	16	*Numenius arquata*	+	3/4/50	Sjölunda	
	12	*Fulica atra*				
	2000	*Larus*	+mE			
		Vanellus vanellus				
	890	*Limosa lapponica*				
1	1000	*Calidris alpina*	+	17/5/50	Sjölunda	
	5	*Calidris temminckii*				
	8	*Tringa totanus*				
1	400	*Cygnus olor*				
	98	*Anas platyhynchos*	+	25/5/50	Sjölunda	
	30	*Tadorna,*				
	100	*Limosa lapponica*				
	35	*Calidris*	+S			
	16+6	*Vanellus*	+mE			
		Tringa (flocks)				
		Larus (flock)				
1	3000	*Vanellus vanellus*	+	11/11/51	Sjölunda	Shooting on 2 ranges.
	250	*Calidris alpina*				
	450	*Charadrius apricarius*				
	12	*Tringa*				
		Anas (flocks)				
		Larus (flocks)				
1	50	*Corvus corone cornix*				Snow, very cold A.E. & M.M.
	200	*Sturnus vulgaris*	+mW	23/3/52	Sjölunda	
		Turdus (flocks)				
		Carduelis (flocks)				
	272	*Vanellus vanellus*				
		Larus, Anas	+			

Number of shots before reaction		Reacting species	React.	Date	Place	Comments
1	10,000	*Vanellus* ⎫	+	28/9/52	Sjölunda	G.M. &
	30	*Charadrius* ⎪				M.M.
		Anas (flocks) ⎪				
		Larus (flocks) ⎭				
1		*Corvus* (flocks) ⎫				G.M. &
		Larus (flocks) ⎬	+	25/10/53	Sjölunda	M.M.
		Anas (flocks) ⎭				
1	300	*Corvus corone cornix* ⎫				
		Corvus frugilegus				
		Corvus monedula				
		Pica pica				
	100	*Columba palumbus*				
	15,000	*Larus argentatus*				
	5000	*Larus ridibundus*				
	50	*Larus canus*				
	1000	*Larus marinus* ⎬	+	28/11/54	Sjölunda	Sk.O.F.
	3000	*Anas platyrhynchos*				exc.
	200	*Anas penelope*				
	500	*Anas crecca*				
	1000	*Bucephala*				
	500	*Aythya*				
	800	*Fulica atra*				
		Mergus, Tadorna				
		Somateria ⎭				

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